National Library of Canada

Cataloguing Branch
Canadian Theses Division

Ottawa, Canada
K1A 0N4

Bibliotheque nationale du Canada

Direction du catalogage
Division des theses canadiennes

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION HAS BEEN MICROFILMED EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ MICROFILMÉE TELLE QUE NOUS L'AVONS REÇUE

A STUDY OF TINTINNIDS AND OTHER PROTOZOA IN EASTERN CANADIAN WATERS WITH SPECIAL REFERENCE TO TINTINNID FEEDING, NITROGEN EXCRETION AND REPRODUCTION RATES

by

Patricia Lee Johansen

Submitted in partial fulfilment for the Degree of Doctor of Philosophy in Oceanography at Dalhousie University, July, 1976.

Approved by:

© PATRICIA LEE JOHANSEN 1977

TABLE OF CONTENTS

ABSTRACT

Tintinnids and other protozoa in eastern Canadian waters tend to be abundant only during summer and fall and to be almost totally absent at other times of the year. Tintinnid abundance is positively correlated with the abundance of nanoplankton on which they primarily feed. The presence of most species of protozoa is marked by huge variations in abundance over very short periods of time (less than a day). Many of the species are quite transient, appearing and disappearing at times within a week. The principal factor controling tintinnid populations in the field is most likely food supply modified by complex interactions with grazers, temperature and reproductive rates.

Tintinnids feeding on nanoplankters can consume 0-75% of their body volume/hr with filtering rates of 0-5 µl/animal/hr. These rates must enable tintinnids easily to control nanoplankton populations in the field.

Tintinnids do not excrete amino acids but may excrete considerable quantities of ammonia (average rate of 6.65×10^{-6} µM ammonia-N/animal/hr) and urea (average rate of 4.43×10^{-6} µM urea-N/animal/hr). These rates are sufficient to supply 25-30% of the nitrogen requirement of the North West Arm phytoplankton and are one to two orders of magnitude higher (on a dry weight basis) than the excretion rates of marine macrozooplankton.

Reproductive rates of tintinnids range from 1 to 9 days, averaging 4 days. These rates were determined for cultures and also for natural populations using abundances and lorica lengths as indicators of reproductively active populations.

1. GENERAL INTRODUCTION

Tintinnids are almost exclusively free-swimming pelagic marine ciliated protozoa which occur at all latitudes, in all seas, and predominantly in the euphotic zone. They are characterized by a conical or trumpet-shaped extensile body which is attached by its inverted apex to the base or side of an enclosing delicate test, called a "lorica". Except at the point of attachment, the soft body is separated from the lorica by an empty space. Tintinnids range in size from 20 to 1000 μ, but most are in the 100-200 μ range.

There are about 750 species of tintinnids in some 62 genera and 13 families. Tintinnid taxonomy has been based almost entirely on the morphology of the lorica since the time of Kofoid and Campbell (1929,1939). Some classification modifications have been made by Corliss (1962) and Marshall (1969). Recent investigations by Gold and Morales (1975a,b, 1976) using scanning electron microscopy may lead to further modifications of tintinnid taxonomy.

Information on tintinnids is relatively sparse, scattered and usually non-quantitative. Many studies concern taxonomy, distribution and general abundance (non-quantitative). See, for example, the number of papers listed in Zeitzschel (1969). Campbell (1926, 1927) did some early studies on cytology. Laval (1971, 1972, 1973) has done some recent studies on tintinnid ultrastructure using electron microscopy. The morphology of the lorica has been studied by Biernacka (1952) and Burkovsky (1973). There are a few notes on vertical migration

in papers by Eggert (1973) and Zaika and Ostrovskaya (1972). Other than this, little appears to have been done. Tintinnids are generally ignored by those who study phytoplankton because they are not phytoplankters and they are ignored by those who study zooplankton simply because they are too small.

The most recent extensive studies of tintinnids (usually of the genus Tintinnopsis) have been those of Gold (1966, 1968, 1969a,b, 1970, 1971, 1973a,b, 1974a,b) and Gold and Morales (1974a,b, 1975a-d, 1976). They have been successful in culturing Tintinnopsis and have investigated the biology, preservation, feeding habits, lorica development and growth characteristics of mass-cultured tintinnids.

Tintinnids are most abundant in neritic waters where they may comprise up to 43% of the microzooplankton (animals smaller than about 200 μ) numerically or about 23% as organic carbon (Beers and Stewart 1970). Although they may represent only a small part of the total plankton biomass, tintinnids may occupy an important place toward the base of the food web in neritic waters. Analyses of samples collected biweekly or weekly from the Northwest Arm (NWA) of Halifax Harbour have shown that the tintinnids can appear in and disappear from the net plankton very rapidly so that a realistic assessment of their role in the food web cannot be made until their distribution and abundance in time are worked out in greater detail. The close proximity of the Dalhousie University campus to the NWA provided a good opportunity to study small scale changes in tintinnid abundance throughout the year.

Tintinnids are said to be second trophic level feeders (Zeitzschel 1967) consuming bacteria, algae, minute flagellates (especially coccolithophorids), dinoflagellates and small ciliates of the nanoplankton (Campbell 1954). They are active hunters rather than merely passive filterers, which may explain why they appear to be more prevalent in highly productive neritic areas rather than in more oligotrophic open ocean waters. It is possible that they may utilize organic aggregates and/or dissolved organic matter. Since tintinnids consume minute food particles, they are probably a basic link in the food web between ultraplankton and organisms such as copepods, which may not be able to handle small particles. There are only two papers dealing with the quantitative aspects of tintinnid feeding; i.e., those of Spittler (1973) and Blackbourn (1974). In order to assess the role of tintinnids in the energy flow of an ecosystem it is necessary to expand our knowledge about the kinds of food consumed by tintinnids and about their feeding rates.

An area of tintinnid biology not even touched upon so far is their interaction with the phytoplankton via their role in regenerating nitrogen which is vital to photosynthesizing phytoplankters. It has been assumed that protozoa, because of their small size, must have high metabolic rates and therefore high excretion rates. There is some evidence for this in the work of Hargrave and Geen (1968) and particularly Johannes (1968) on phosphorus regeneration, but nothing is known of nitrogen regeneration by tintinnids. The large

abundances of tintinnids to be found at times in the NWA have provided an opportunity to gain some first order approximations of the nitrogen-releasing capabilities of these protozoans.

In order to gain increased knowledge of the role of tintinnids in a natural ecosystem, the objectives of this study were as follows:

1. To determine the distribution, abundance and species succession of tintinnids and other protozoa in the NWA with particular regard to small scale temporal variations.

2. To determine feeding rates of the major tintinnid species found in the NWA.

3. To obtain some information about the types and quantities of nitrogen-containing compounds excreted by tintinnids.

2. TINTINNID (AND OTHER PROTOZOA) ABUNDANCE, DISTRIBUTION AND SEASONAL CYCLES IN THE NORTHWEST ARM OF HALIFAX HARBOUR

INTRODUCTION

There is a substantial number of papers dealing with the distribution of tintinnids (and other protozoa) in marine waters (see Zeitzschel's rather extensive 1969 list of references as well as Loeblich and Tappan 1968). However, the vast majority of these are taxonomic studies and list the species as only "present, rare, common, very abundant", etc., primarily because the collections were made using nets, usually with meshes of >150 μ. Since the largest tintinnid (Parafavella) has a diameter of only about 60 μ, such nets would allow the escape of most tintinnids. Non-loricate protozoa (and indeed some loricate forms such as the strombidia) are certainly destroyed by nets.

Some attempts to quantify tintinnid abundances have been made by the following workers:

(a) Hensen (1887); net collections of Parafavella from the North Sea,
(b) Brandt (1907); net collections of total tintinnids from the Irminger Sea,
(c) Lohmann (1908); centrifugation samples of Tintinnopsis nucula from Kiel Bay,
(d) Lackey (1936); Utermohl samples of Tintinnopsis beroidea and total ciliates from Woods Hole,
(e) Halldal (1953); Utermohl samples of Parafavella from the Norwegian Sea,
(f) Vitiello (1964); Utermohl samples of total tintinnids from the Bay of Algiers,
(g) Zeitzschel (1967); net collections of total tintinnids from North Atlantic weather stations,
(h) Mulford (1973); Utermohl samples of total tintinnids from Chesapeake Bay,
(i) Hedin (1974); net collections of total tintinnids from a Swedish fjord.

Most of these studies suffer from (a) long time intervals between sampling (e.g. Hedin, Zeitzschel, Mulford) or (b) covering only very short periods of time (e.g. Lackey, Vitiello). However, they generally show one important feature: great fluctuations in abundance (and composition) of the tintinnid fauna during the sampling period.

In order to assess the impact of this group of organisms on the environment and on other organisms, it is necessary to have a better idea of which species occur, when they occur and in what abundances. The desire for such information prompted this study of protozoan taxonomy, distribution and abundance in the Northwest Arm (NWA).

METHODS

During 1972 and the summer of 1973, 500-ml samples were taken using 5-l Niskin bottles (and preserved with 1% Champy's fixative) from 0, 6, 12 and 25 m at Station A (off Ferguson's Cove) and from 0, 4, 8 and 13 m at Station E (midway between the Dingle and Little Gut). Figure 1 shows the location of these NWA stations. The sampling interval was two weeks (one week during the spring and fall phytoplankton blooms). A total of 312 samples were taken for the enumeration of phytoplankton and protozoa using the Utermohl method (1931). For the enumeration of protozoa and large phytoplankters, specimens in 300 ml of the preserved sea water sample were allowed to settle and were then counted at 100x using a Wild inverted microscope. Enumeration of the more numerous nanoplankton

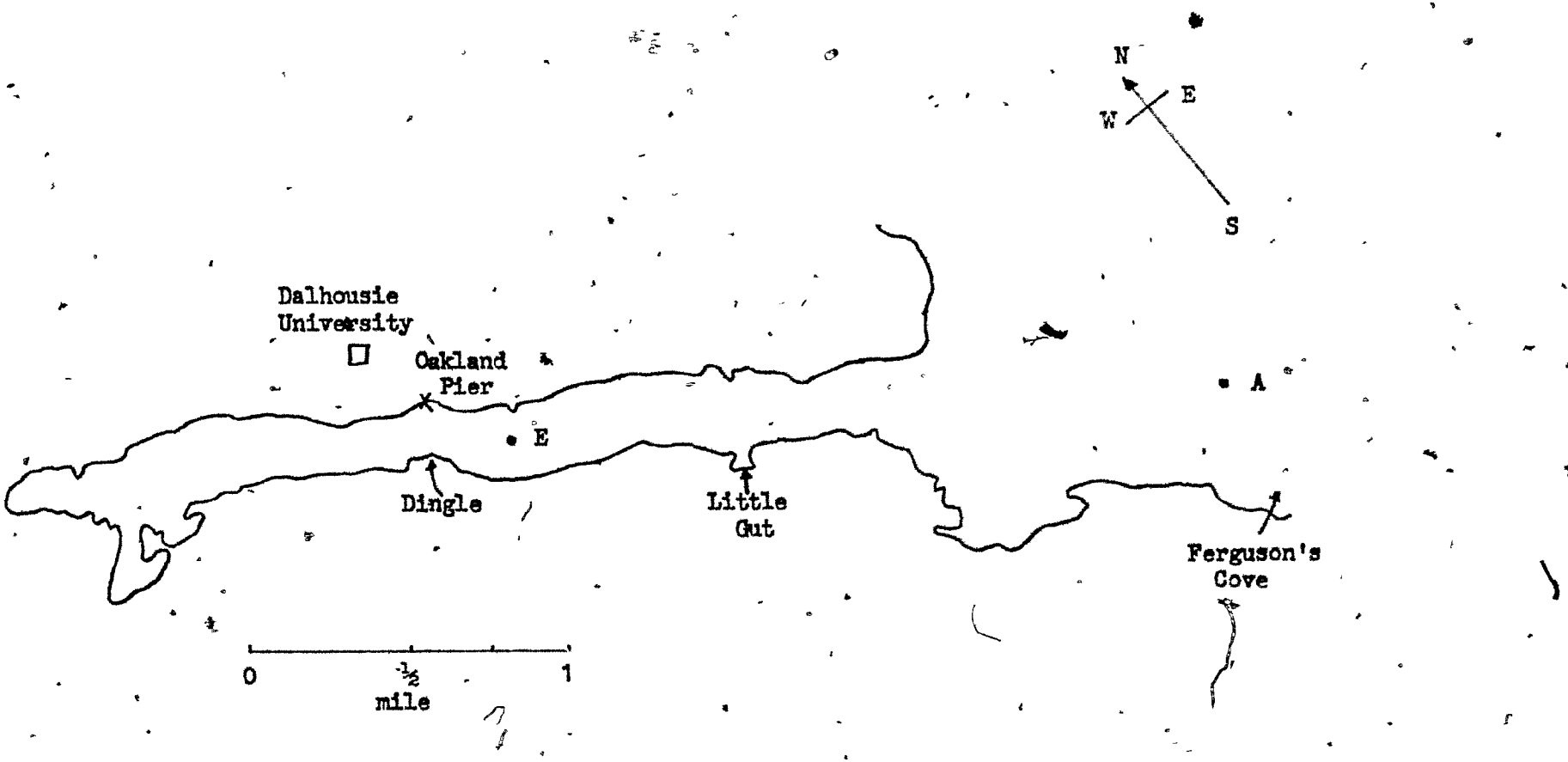


Figure 1. Station locations in the Northwest Arm of Halifax Harbour

required the settling of 10-50 ml and counting at 400x. Salinity and temperature were also recorded for each sampling date.

During 1974 a net tow was taken every week at Station E using a 30-cm, 10 μ mesh net. The tow was vertical and lasted approximately 5 minutes. Salinity and temperature were also recorded and a bottle sample was collected (and preserved) from 5 m. Net phytoplankton as well as protozoa were noted but the organisms were not enumerated, although the five most abundant phytoplankton species were noted as such. Protozoa were enumerated from the preserved bottle samples.

From 11 October 1974 until 12 October 1975 (except for the period 17 Dec 1974-23 Jan 1975) daily surface bucket samples were taken (and preserved) at daylight low tide at the Oakland Pier (directly opposite Fleming Park Tower at the Dingle, see Fig. 1). 200 ml were settled and the protozoa identified and enumerated at 100x. From 15 February until the end of the sampling period the five most abundant phytoplankters were also noted, but the phytoplankton were not counted. Water temperature was also recorded.

RESULTS

A Note about the Phytoplankton.

In the NWA spring and fall dinoflagellate blooms generally follow spring and fall diatom blooms. Table 1 indicates the phytoplankton species involved in the blooms observed in 1972, 1974 and 1975. Figs. 2 and 3 show the abundance of diatoms,

dinoflagellates and nanoplankton for 1972 and the summer of 1973. The sequence of events is the same from year to year although the time of occurrence may shift backward or forward. The summer phytoplankton is completely dominated by nanoplankton.

The Protozoa:

Table 1. Diatom and dinoflagellate bloom species: 1972, 1974 and 1975

DATE	DIATOMS	DINOFLAGELLATES
1972		
Mar-mid Apr	Chaetoceros socialis + Thalassiosira	
late Apr		Gyrodinium fusiforme
early June	Leptocylindrus danicus	
July		Gymnodinium rotundatum
late Sept	Skeletonema costatum	
early Oct		Gonyaulax unicornis
1974		
Apr-mid May	Chaetoceros socialis + Chaetoceros debilis	
early July	Skeletonema costatum	
late July		Dinophysis norvegica + Ceratium longipes
late Sept-late Oct	Rhizosolenia fragilissima	
Nov		Ceratium longipes + Distephanes speculum*
1975		
Jan-early Mar	Distephanus speculum*	
late Mar-Apr	Chaetoceros socialis + Thalassiosira	
late Sept	Skeletonema costatum	
June-Oct		Dinophysis norvegica + Ceratium longipes

* Silicoflagellate

Forty-five species of protozoa were identified in the NWA during 1972-75, 40 of which were ciliates, 25 being tintinnids

Figure 2. Abundance of diatoms and dinoflagellates: 1972 and summer of 1973 (circles indicate 1973 values).

Figure 3. Abundance of nanoplankters and tintinnids: 1972 and summer of 1973 (circles indicate 1973 values).

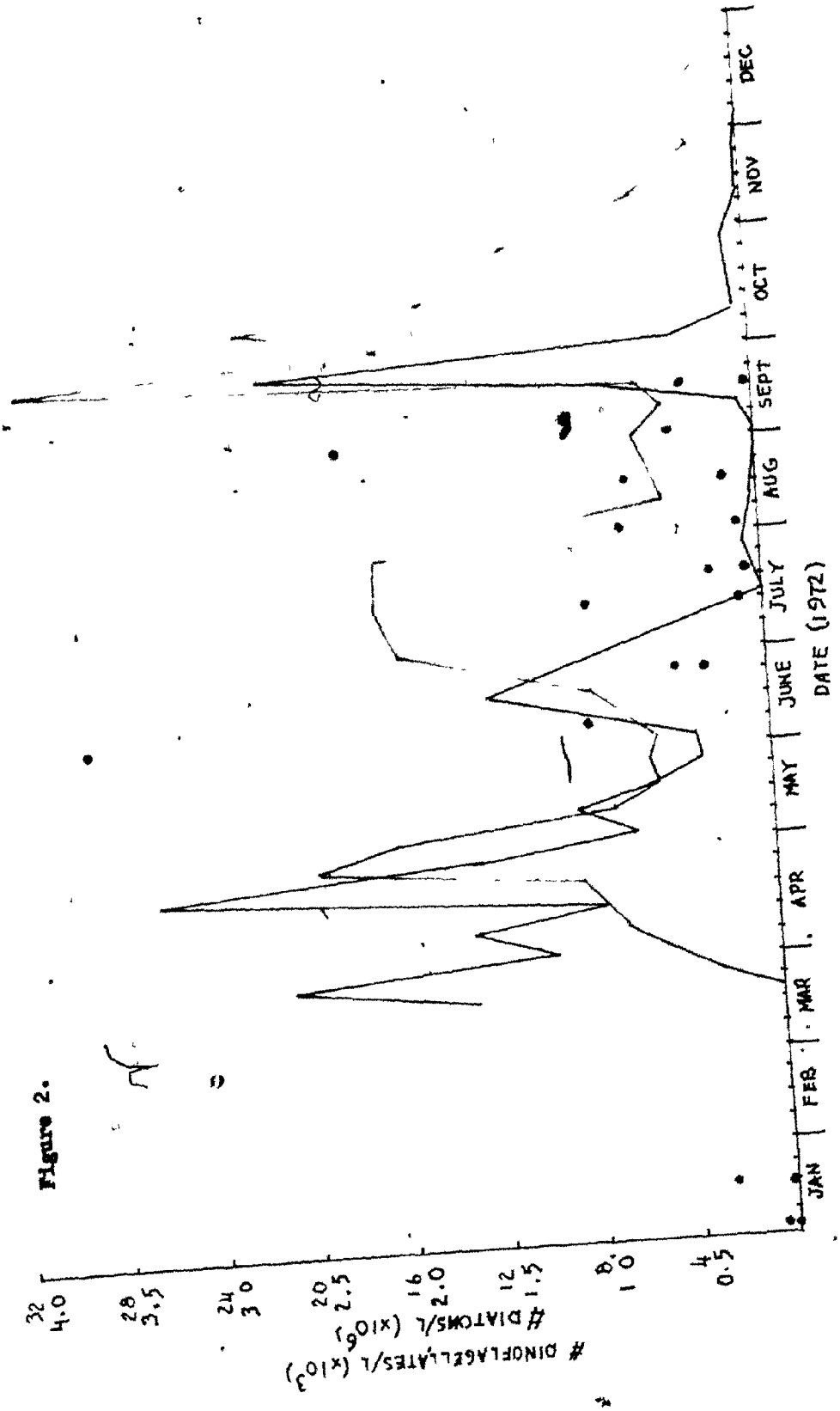
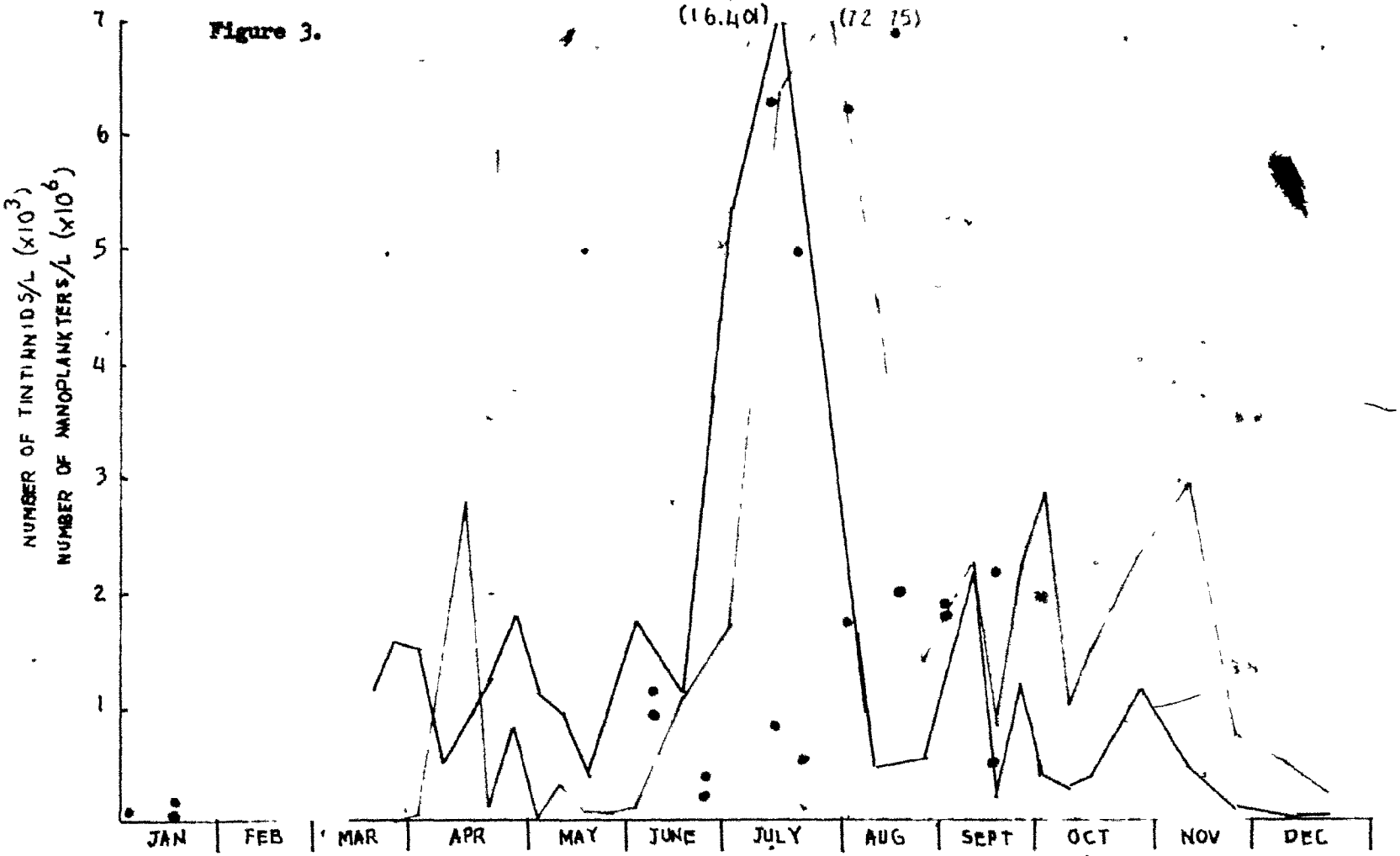

JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1972)
DINOFLAGELLATES/L (x10³)
DIATOMS/L (x10⁶)
32 4.0
28 3.5
24 3.0
20 2.5
16 2.0
12 1.5
8 1.0
4 0.5

Figure 2.

Figure 3.


(16.401)
(72 75)
NUMBER OF TINTINNIDS/L (x10³)
NUMBER OF NANOPLANKTERS/L (x10⁶)
7
6
5
4
3
2
1
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

and 7 being strombidia. Only 16 species (all ciliates) were sufficiently abundant for a long enough period of time to be considered important. These 16 species are marked with an asterisk in Table 2, which lists all species identified and the months of occurrence.

Fig. 4 shows the abundance of total protozoa during 1972-75, based on biweekly or weekly samples. Table 3 indicates the protozoan species involved in the peaks observed. In general, the protozoa experience a minor peak in early March followed by a decrease until summer during which time the protozoa reach their maximum abundance. A decline in numbers during October is followed by another burst of growth in November, smaller than the summer peak but larger than the early spring peak. This distribution is particularly clear in the graphs of daily abundance (Appendix A Figs. 1-4).

Little is known about the strombidia. Although these oligotrichous ciliates possess loricae, they are very fragile. I have only rarely seen them in net hauls but counts from settled bottle samples reveal that they are usually the most abundant protozoans present. During the first four months of the year they commonly comprise 90-100% of the protozoa (Fig. 5). During the summer they are equal in number to tintinnids and in the fall they again dominate the protozoa after the final tintinnid bloom. The numerical abundance of the strombidia is presented in Fig. 6 and Appendix A, Figs. 5-8.

Five strombidia species are commonly found in the NWA. These are shown in Appendix B figures 1-5. The abundance of

Table 2. North West Arm protozoan species and their months of occurrence

SPECIES	1972	1973	1974	1975
Phylum PROTOZOA				
Subphylum PLASMODROMA				
Class SARCODINA				
Subclass RHIZOPODA				
Order TESTACIDA				
Difflugia oblonga	May			June
Euglypha laevis				July-Sept
Order FORAMINIFERA				
Globigerina aequilateralis	Mar-May Aug-Dec	June-Sept	Nov	Jan,June
Subclass ACTINOPODA				
Order RADIOLARIDA				
Acantrostaurus pallidus	Dec			
Subphylum CILIOPHORA				
Class CILIATA				
Subclass HOLOTRICHIDA				
Order GYMNOSTOMATIDA				
Cyclotrichium meunieri*	Mar-Dec	Jan,June-Sept,Dec	Jan-Dec	Jan-Oct
Didinium nasutum			Apr	Mar-May
Mesodinium pulex*			May,June, Oct,Nov	Feb-Sept
Mesodinium rubrum	June		Nov,Dec	May-Aug
Tiarina fusus				Apr,May July-Sept
Order HYMENOSTOMATIDA				
Frontonia marina	June		Nov,Dec	Jan-Oct
Subclass SPIROTRICHA				
Order OLIGOSTICHIDA				
Strombidium sp.*	Mar-Dec	Jan, June-Sept	Mar-June Sept-Dec	Jan-Oct
Strombidium acuminatum			Oct,Nov	Mar-June
Strombidium calkinsi*	Mar-June, Aug-Nov	June-Sept	Mar-June, Aug-Oct	Jan-Oct
Strombidium conicum*	Mar-Aug, Oct-Dec	Jan,Aug, Sept	Oct	Jan-Oct
Strombidium ovale			Oct	Apr,May
Strombidium strobilus*	Mar-July, Nov,Dec	Jan,June, Aug,Sept	Mar,May, June,Sept Oct,Dec	Jan-Aug, Oct
Strombidium sulcatum*	Mar-Dec	Jan,June-Sept,Dec	Jan-Dec	Jan-Oct
Tontonia gracillima*	Mar,May-Dec	Jan,June-Sept	Mar-June, Sept-Dec	Jan-Oct
Order TINTINNIDA				

Table 2. (continued)

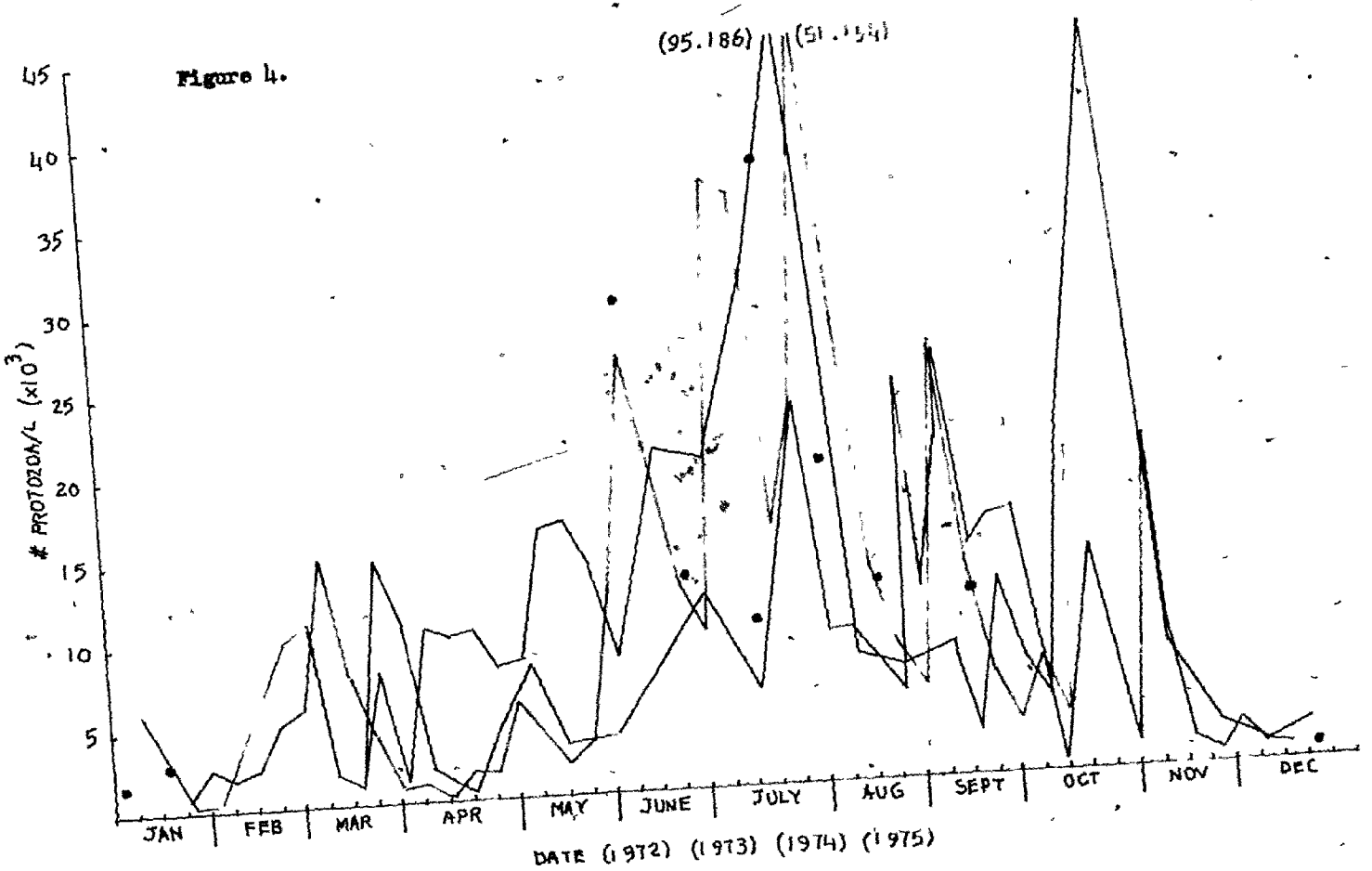
SPECIES	1972	1973	1974	1975
Acanthostomella norvegica				Mar
Coxliella ampla				May
Dadayiella bulbosa				Sept
Dictyocysta reticulata	May	July		
Helicostomella subulata*	June-Dec	Jan,July-Sept	Mar,June-Dec	Jan-Mar June-Oct
Leprotintinnus pellucidus*	May	June-July	Apr-June, Dec	May,June
Parafavella gigantea*	Apr,May, July-Sept	July-Sept	Aug-Oct, Dec	Feb,Aug-Oct
Parafavella parumdentata	Apr,May, Aug,Oct-Dec	Jan,Aug	May,Nov	Feb
Parundella minor	Mar,Apr			Sept
Proplectella perpusilla	May-Aug, Dec		Nov,Dec	
Proplectella tumida			Nov	Feb,July, Oct
Ptychocylis drygalski	Apr,Dec	July		Apr,May
Salpingella acuminata			Dec	Oct
Salpingella curta			Oct	
Tintinnopsis cylindrica				Sept
Tintinnopsis karajacensis*	Apr,June, July		Mar-June	Jan-Aug
Tintinnopsis parvula*	Mar-Dec	Jan,June-Sept,Dec	Jan,Apr-Dec	Jan-Oct
Tintinnopsis nitida	June,July		Oct-Dec	Aug
Tintinnopsis sacculus*			Mar,May-July,Sept	May-Oct
Tintinnopsis strigosa*	Apr,June, July,Oct	Jan,June-Aug	Mar-June, Aug,Oct-Dec	Jan, Mar-July, Sept,Oct
Tintinnopsis vasculum			Mar-May, Oct	Mar-July
Tintinnopsis wailesi			Nov	
Tintinnus tubulosus	Dec	June,Aug, Sept		Sept,Oct
Undella columbiana	Aug		Nov,Dec	Jan,Feb, Oct
Undellopsis marsupialis				Sept
Order HYPOTRICHIDA				
Euplotes sexcostatus*	Apr,May, Sept-Dec	Jan,July	Nov,Dec	Mar-Sept
Class SUCTORIA				
Order SUCTORIDA				
Trichophrya columbiae				May,June

Figure 4. Abundance of protozoa: 1972-1975

Figure 5. Abundance of strombidia expressed as percentage of total protozoa: 1972-1975

Figure 6. Abundance of strombidia: 1972-1975

Figure 4.


(95.186)
(51.154)
45
40
35
30
25
20
15
10
5
PROTOZOA/L (x10^3)
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1972) (1973) (1974) (1975)

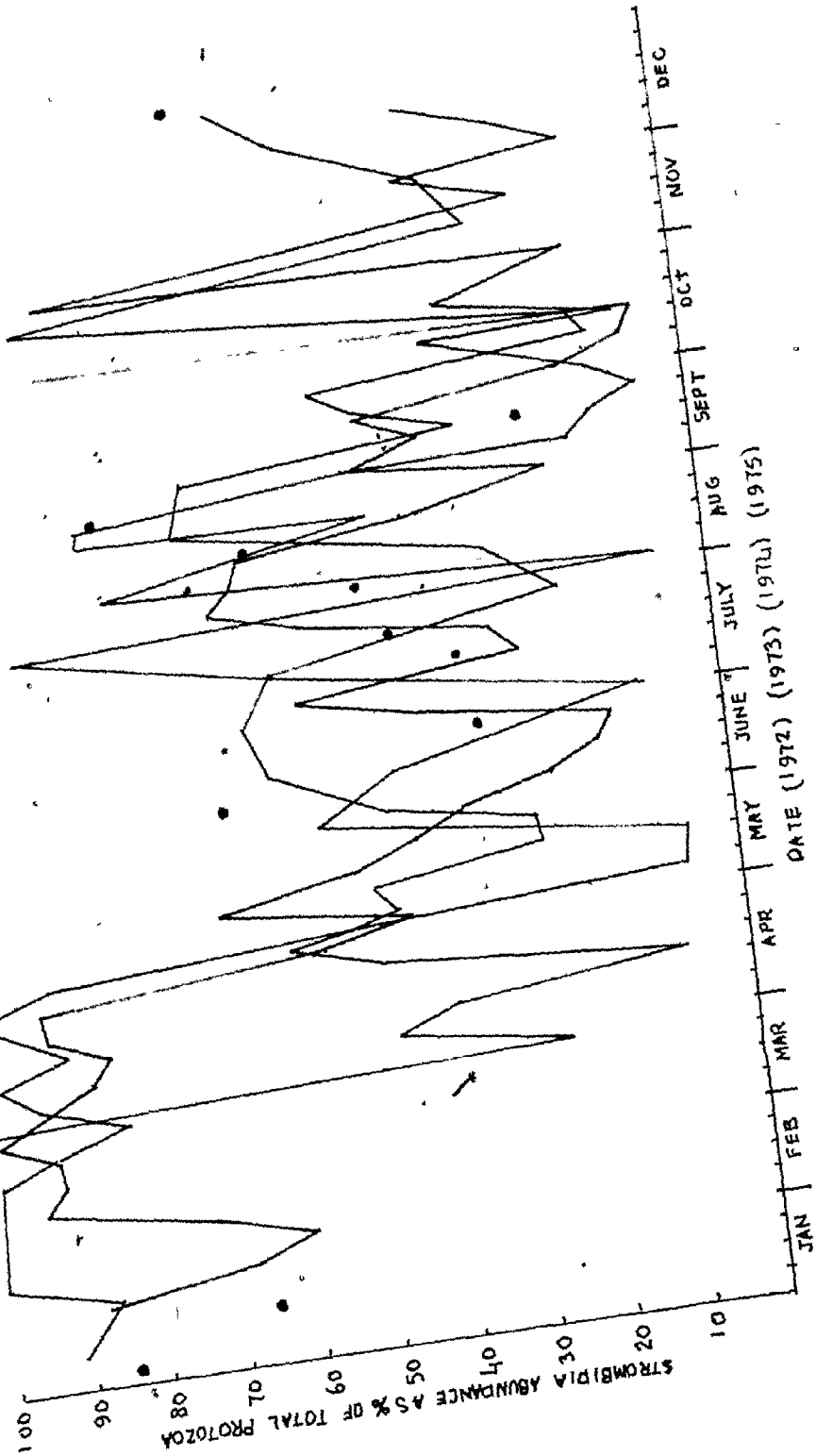
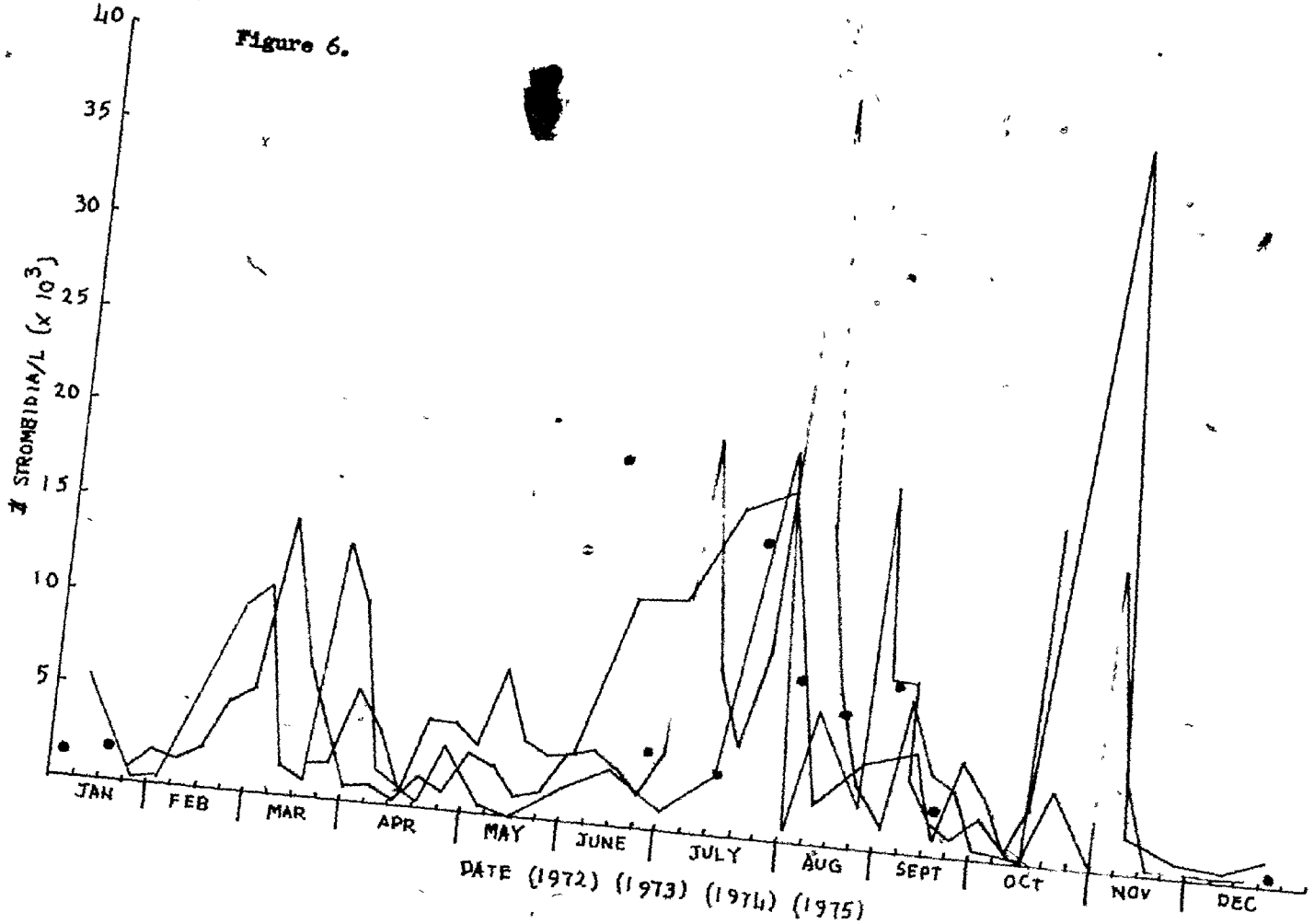

STROMBIDIA ABUNDANCE AS % OF TOTAL PROTOZOA
100
90
80
70
60
50
40
30
20
10
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1972) (1973) (1974) (1975)

Figure 5.

Figure 6.


40
35
30
25
20
15
10
5
STROMBIDIA/L (x 10^3)
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCt
NOV
DEC
DATE (1972) (1973) (1974) (1975)

the different strombidia species is shown in Appendix A, Table 1, and Appendix A, Figs. 9-12. Note that for the 1975 data, only the periods of significant abundance are represented. In general, strombidia succession is as follows:

S. sulcatum (Mar) → Strombidium sp. (Apr) → S. calkinsi (early May) → S. conicum (late May-June) → S. strobilus (early June) → S. sulcatum (late July-Aug) → S. calkinsi (Sept) → S. sulcatum (late Oct).

The numerical abundance of tintinnids is shown in Fig. 3 and Appendix A, Figs. 13-17. There is usually a minor peak in spring followed by a decline with maximum numbers occurring during several summer peaks. Sometimes a minor fall burst of growth is observed. Note the differences is vertical scale on the daily graphs.

Seven tintinnid species are common to the NWA. These are shown in Appendix B, Figs. 6-12. Distributions of individual tintinnid species are shown in Appendix A, Table 2, and Appendix A, Figs. 18-21. Tintinnid succession is as follows:

T. strigosa (May) → T. karajacensis (first week in June) → L. pellucidus (second week in June) → T. sacculus (third week in June) → T. parvula + H. subulata (July) → H. subulata + P. gigantea (Aug) → H. subulata (Sept) → T. parvula (Oct).

The four remaining important protozoa found in the NWA are pictured in Appendix B, Figs. 13-17, and their seasonal occurrence is shown in Appendix A, Table 1, and Appendix A, Figs. 22-26.

DISCUSSION

Fig. 7 shows the surface temperature in the NWA during

Figure 7. North West Arm surface water temperature: 1972-1975

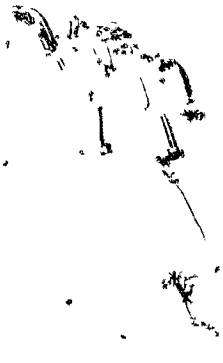
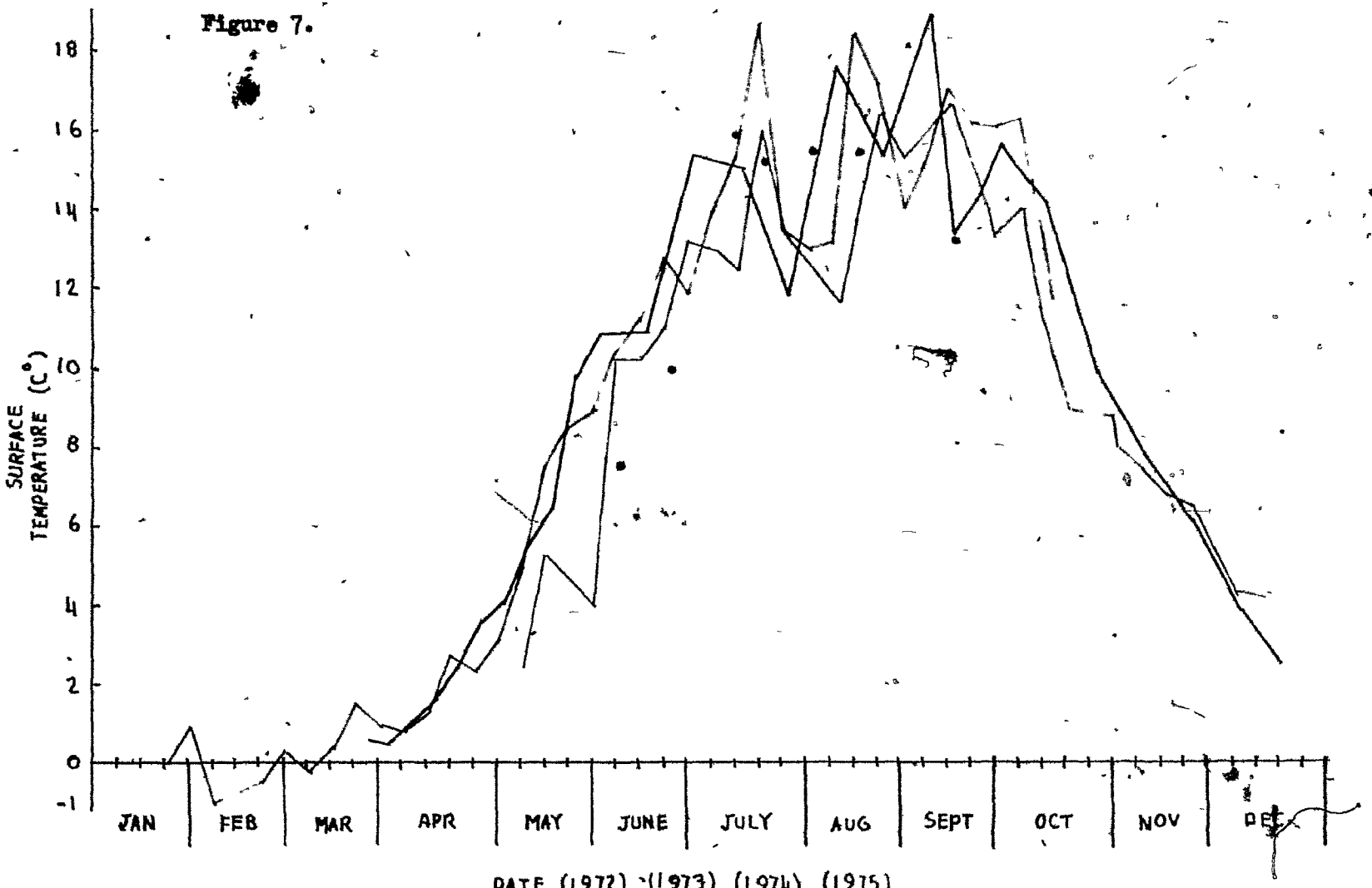


Figure 7.


SURFACE TEMPERATURE (C°)
18
16
14
12
10
8
6
4
2
0
-1
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1972) (1973) (1974) (1975)

the sampling period. In 1972 and 1975 the yearly maximum of protozoa abundance (Fig. 3 and Appendix A, Figs. 1-4) corresponded with mid-summer temperature minima. There may be one or more of these temperature minima, commonly in late July or August. They are local wind-drived upwelling events in which the warm surface layer is removed seaward and is replaced by cooler and generally more saline subsurface water from offshore. The protozoa-temperature relationship does not hold for 1974, perhaps because the water temperature was lower than normal the entire year. It does not hold for the summer of 1973 either, when the mid-summer temperature minimum did not occur at all and protozoan numbers were unusually low. The situation is much the same for the strombidia (Fig. 6 and Appendix A, Figs. 5-8). Note here, though, the presence of a spring maximum which occurs when water temperature is very low (about 1°C). The same is also true for tintinnids (Appendix A, Figs. 2, 18-22). In the 1975 data, there are indications that Cyclotrichium also prefers the mid-summer cool periods and that Tontonia prefers the cooler waters of early summer. Mesodinium is found during spring warming but also occurs in late July, which may suggest an optimum temperature for it of 11-12 ° C. Bary and Stuckey (1950) noted that Cyclotrichium blooms in Wellington Harbour (Australia) declined when the temperature exceeded 16° C.

Although a total of 45 protozoan species were identified, there were never more than about half this number present at

any one time (Fig. 8). Only about one-third of the 25 tintinnid species were found in the plankton at any one time (Fig. 9). Gold and Morales (1975) also found that less than half the total number of tintinnid species occurring in the New York Bight were present at any one time.

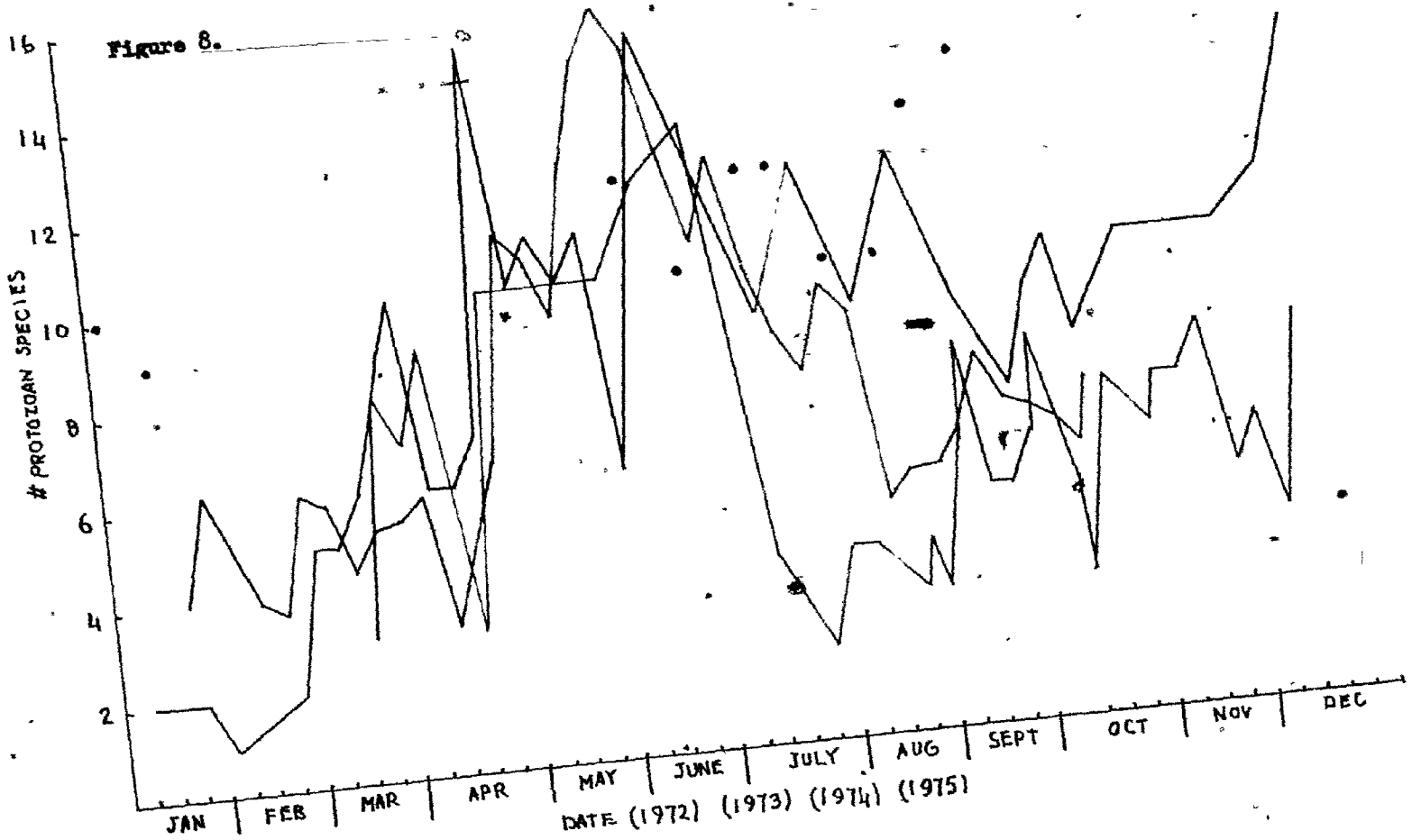
Yearly variations in the number of species present is similar for tintinnids and for total protozoa, which is reasonable since tintinnids comprise the majority of the species observed. Few species are found during winter. The number of species begins to increase in spring, reaches a maximum in late May or early June, and drops off gradually during the remainder of the summer. A slight increase during the fall often occurs. The maximum number of protozoan (and tintinnid) species occurs well before the temperature maximum. In the waters off New York Gold (1974) found that the maximum number of tintinnid species occurred in the fall, well after the yearly temperature maximum in that area. He suggested that optimum temperature and adequate food supply in the fall produce this distribution. I suspect the same is true for the NWA, despite the difference in time of occurrence. Zeitzschel (1967) also noted that the tintinnid maximum occurs before the temperature maximum in the North Atlantic, as did Mulford (1972) in Chesapeake Bay.

Although the number of species present may be high when protozoan abundance is high, this is not always the case. In fact, the maximum protozoan abundance occurs when the number of species is quite low. If the Shannon-Wiener formula (Pielou

Figure 8. Number of protozoan species: 1972-1975

Figure 9. Number of tintinnid species: 1972-1975

Figure 8.


PROTOZOAN SPECIES
16
14
12
10
8
6
4
2
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1972) (1973) (1974) (1975)

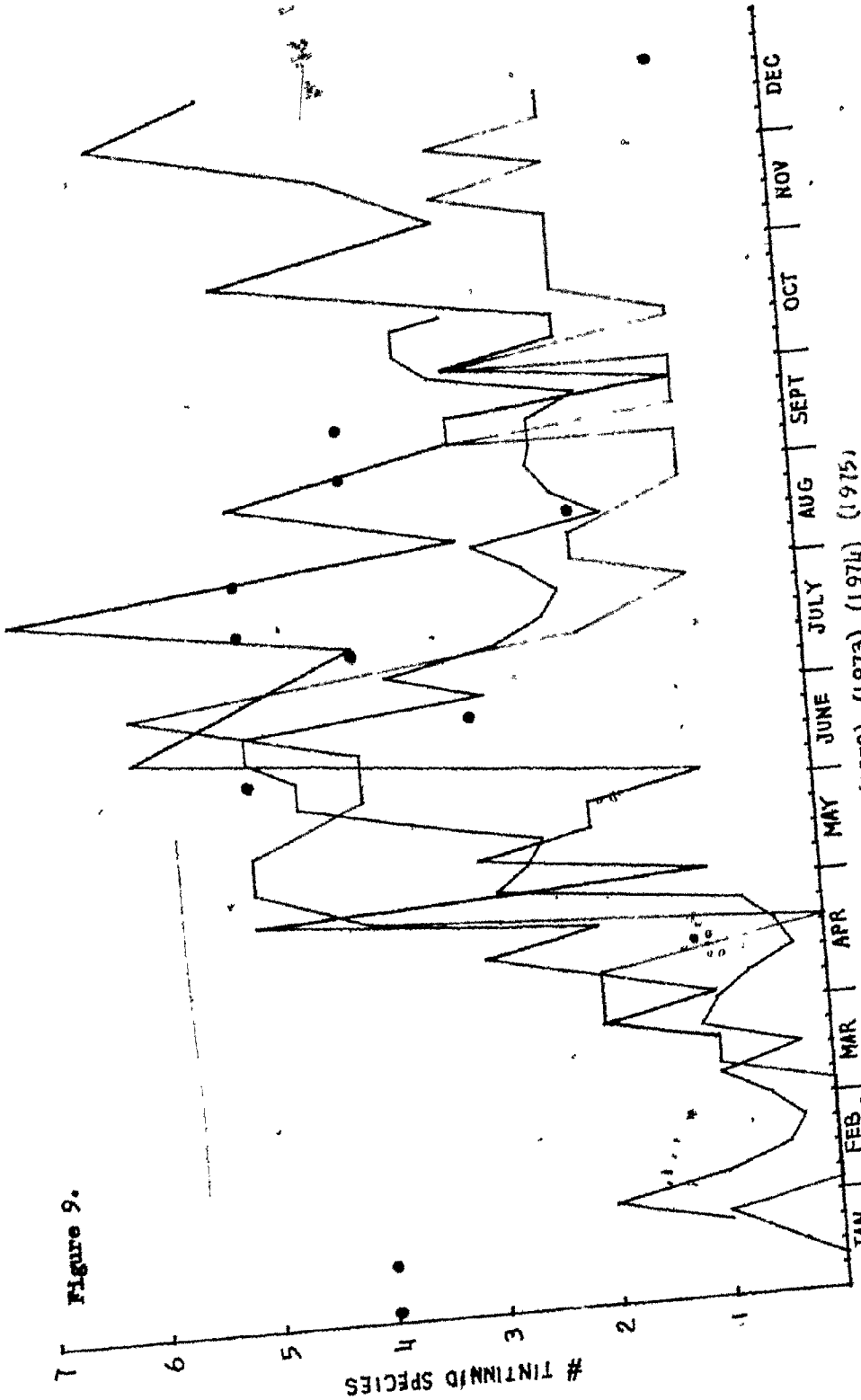

TINTINNID SPECIES
7
6
5
4
3
2
1
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1972) (1973) (1974) (1975)

Figure 9.

1974) is used to calculate species diversity indices, it is clear that high abundance is usually associated with low diversity (Fig. 10). The Shannon-Wiener diversity index is calculated as follows:

$$H_s = - \sum_{i=1}^{s} p_i \ln p_i \; ; \quad \text{where:}$$

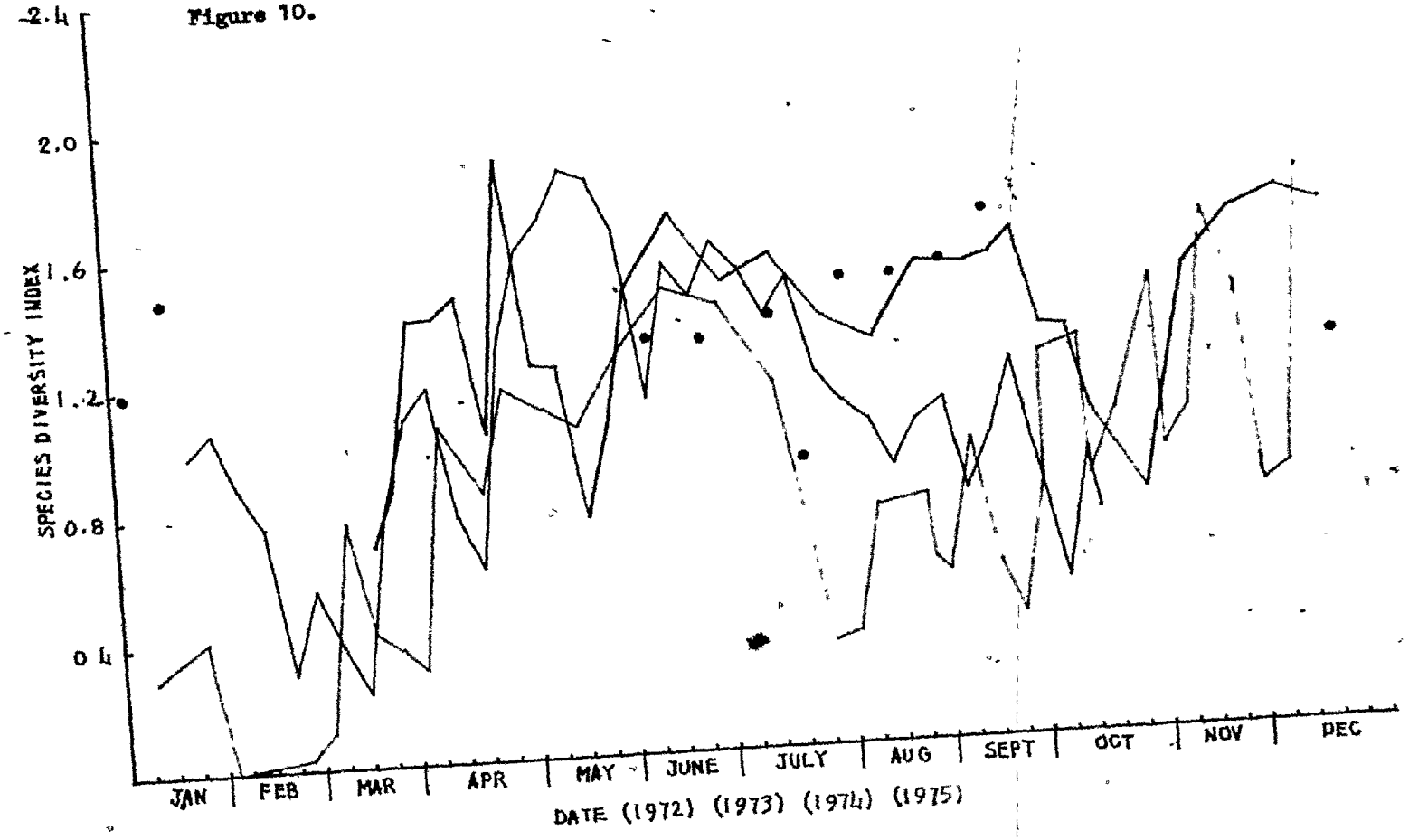
H_s = the diversity index of the sample
s = the number of species in the sample
p_i = the relative abundance of the i th species measured
$\ln p_i$ = the natural log of p_i

Thus this index takes into account not only the number of species but also the relative abundance of each species. This means that in the NWA there are a large number of rather rare species. The protozoa blooms consist of: (a) Cyclotrichium (Oct-Nov 1974); (b) a Strombidium (Feb-Mar 1974); (c) any one of the tintinnid species (July 1972); (d) a combination of any two of the groups (S. sulcatum and H. subulata in Aug 1975): or even (e) all three (Cyclotrichium, S. sulcatum and H. subulata in July 1975). This dominance of the community by a very few species has also been noted for phytoplankton (Mulford 1972) and it occurs among the net phytoplankton of the NWA as well. Vitiello (1964) found many tintinnid species in the Bay of Algiers but only three species could be considered as common or abundant:

It is fairly common to find several species of the same group in the water column at the same time. This is probably

Figure 10. North West Arm species diversity indices: 1972-1975

Figure 10.


2.4
2.0
1.6
1.2
0.8
0.4
SPECIES DIVERSITY INDEX
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1972) (1973) (1974) (1975)

made possible by most of the species being of the "fugitive" sort during most of the time with only one species blooming at a time. However, one bloom can displace another in rapid succession, as in 1975 when T. strigosa bloomed May 22-27; T. sacculus bloomed May 27-June 5; and T. karajacensis bloomed June 7-15. Vitiello (1964) reported that in the surface water of the Bay of Algiers Favella azorica reached its maximum abundance on Dec 16 only to be replaced by Tintinnopsis beroidea on Dec 23 which was in turn replaced by Stenosemella ventricosa on Jan 5.

Data from 1972 show that when two species in the same group are abundant at the same time they tend to occupy different regions of the water column or tend to be more abundant at one station that at another. For example, H. subulata and T. parvula bloomed at the same time (26 July 1972) but the latter was much more abundant toward the bottom of the water column (Fig. 11). The same was true of T. karajacensis and T. strigosa (23 May 1975), the latter occurring at a lower depth (6 m) at Station A and the surface at Station E, the opposite being true of T. karajacensis. Again, T. strigosa and L. pellucidus have different depth preferences. H. subulata and P. gigantea usually occurred together (although Helicostomella was always much more abundant) and their distribution with depth was very similar. However, they belong to different genera and the great difference in size indicates that they may feed on different-sized particles.

Figure 11. Relative abundance of protozoa at various depths at NWA Stations A and E (black = Station A; red = Station E)

Figure 11.

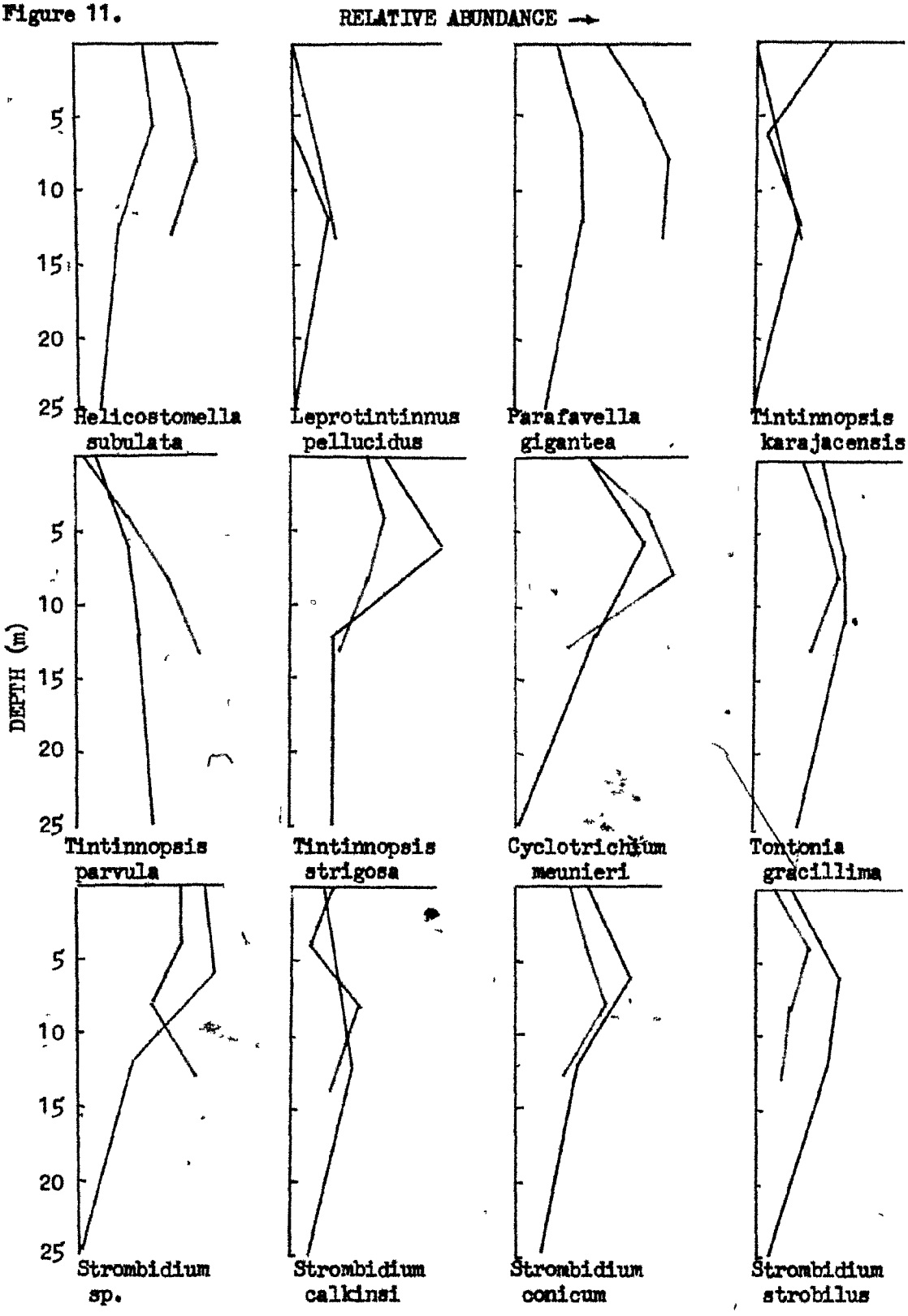

RELATIVE ABUNDANCE →
DEPTH (m)
5
10
15
20
25
Helicostomella subulata
Leprotintinnus pellucidus
Parafavella gigantea
Tintinnopsis karajacensis
Tintinnopsis parvula
Tintinnopsis strigosa
Cyclotrichium meunieri
Tontonia gracillima
Strombidium sp.
Strombidium calkinsi
Strombidium conicum
Strombidium strobilus

Fig. 11 also reveals that Helicostomella and Parafavella prefer inshore water while T. strigosa and possibly T. karajacensis are offshore species. This fact may indicate that this strain of Parafavella gigantea is endemic to the NWA and casts doubt on the belief that Parafavella is strictly a cold-water species (Ling 1965) and is merely intruded into this area from higher latitudes. Besides, it is seen to undergo division in this area so it is not merely a relict of the North. Note also that the tintinnids are most common in the upper part of the water column (0-8m) and that this is also the area of maximum nanoplankton abundance (Fig. 12).

The depth distribution of the strombidia is similar at both stations although they all tend to be slightly more common offshore. It is common for all five species to occur together (particularly in May-July) but the group is almost always dominated by S. sulcatum. During 1972-73 Strombidium sp. seemed to have been usually more abundant than S. sulcatum, but by 1975 this trend was reversed with S. sulcatum being almost always more abundant than Strombidium sp. The reason for this is unknown. Also, T. sacculus did not occur in 1972-73 but was fairly common in 1974-75 while Ptychocylis drygalskii, Undella columbiana and Parafavella parumdentata, which were found in 1972-73, have disappeared from the NWA in the past two years. These appearances and disappearances may indicate long-term subtle changes in the environment of the NWA or perhaps these distribution changes are influenced by isolated intrusions of water from offshore.

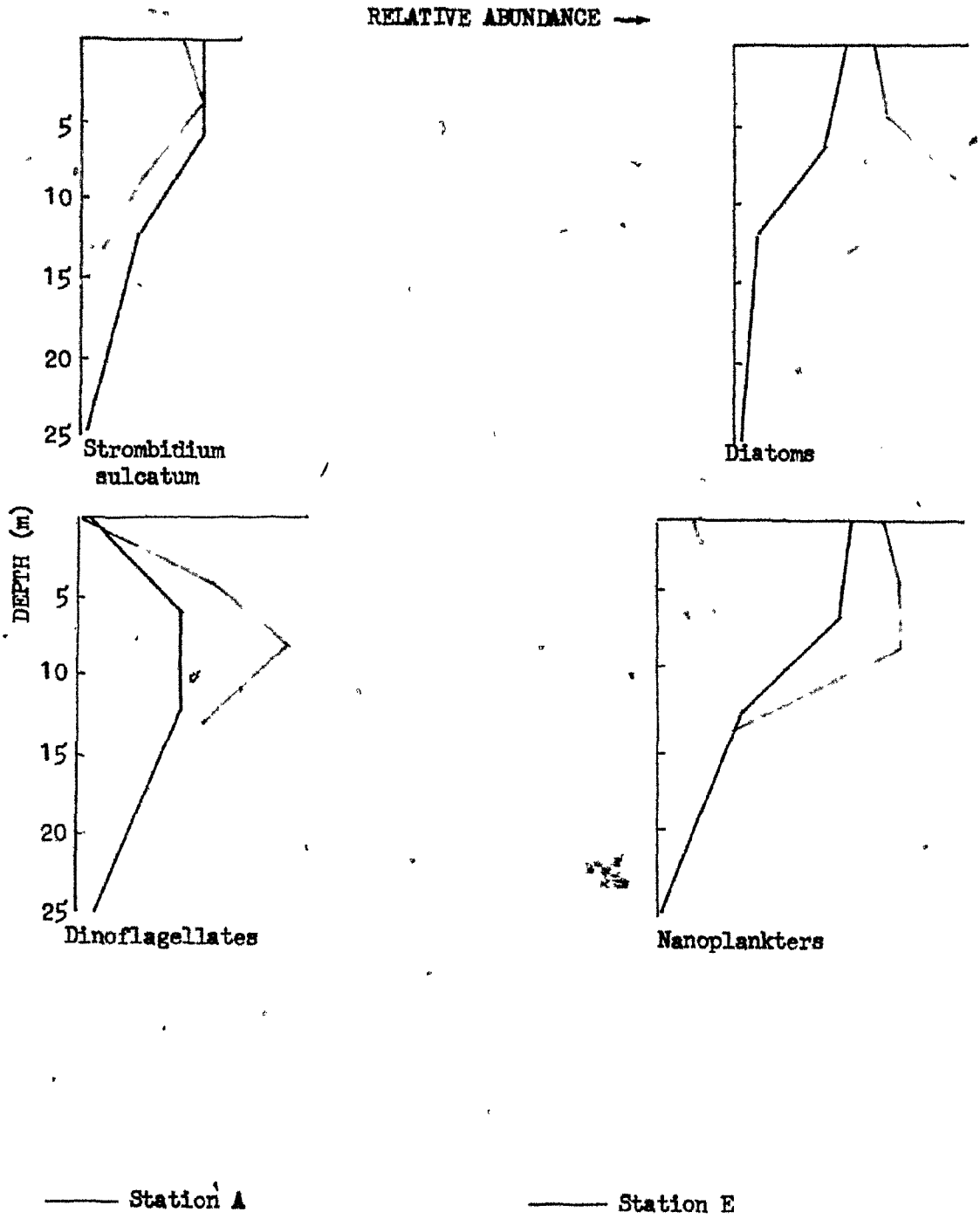


Figure 12. Relative abundance of protozoa and phytoplankters at various depths at NWA Stations A and E

The depth distribution of Cyclotrichium is similar to that found in Wellington Harbour, Australia (Bary and Stuckey 1950), with its subsurface (4-8 m) maximum, although it blooms more often in June-July and Oct-Nov in Halifax as opposed to April and August in Australia. This organism may be a common inshore form, as the Scotian Shelf data indicate only low abundance offshore. This was the dominant protozoan in Nain Bay, Labrador in late October 1973. It is a curious organism, being covered by greenish-maroon convo-convex platelets (chromatophores?) lying beneath the pellicle. Bary and Stuckey (1950) were not able to find either cytostome or food vacuoles in this organism so its mode of nutrition is in question. Still, it is a most successful organism in the NWA and should perhaps be studied further once the problem of its delicate nature can be solved.

Euplotes is generally considered to be a benthic species. It was only rarely encountered in the plankton at Station E. However, at the Oakland Pier station during 1975 (Apr-July) it was found in the plankton in substantial numbers several times.

It is also possible that the groups delimit their niches by feeding on different types of organisms. The two most common strombidia are quite small and may feed on bacteria. Spittler (1973) has determined that Tintinnopsis do not generally take in particles smaller than 2 μ or particles larger than about half thear oral diameter (i.e., <20 μ in most

cases) so that they probably feed on the nanoplankton rather than on bacteria (which are quite detrimental to tintinnids in culture). Cyclotrichium may be saprophitic; Euplotes may not feed in the plankton at all.

Fig. 2 showed a conspicuous relationship between tintinnid abundance and nanoplankton abundance in the NWA. Qualitative data from daily sampling during 1975 confirm this pattern. Tintinnid maxima generally occur after dinoflagellate maxima (which occur after diatom maxima) and immediately lag behind and overlap the nanoplankton peaks in a classic predator-prey pattern.

The major summer tintinnid maximum, which is comprised almost exclusively of Helicostomella and Tintinnopsis parvula, coincides with the mid-summer temperature minimum (Fig. 7), which led me to suspect that the tintinnids were merely being upwelled or driven inshore from offshore, especially since the absence of the temperature minimum in 1973 was accompanied by an absence of tintinnids as well. However, the offshore data clearly indicate that the blooms of both species originate inside the NWA. They occur at Station E first and are much more abundant there. The work of Hedin (1974) also indicates that Tintinnopsis and H. subulata are inshore species. The Scotian Shelf data also indicate the very low abundance of these species offshore.

I then thought that the upwelling water produced the nanoplankton bloom which in turn made the tintinnid burst of growth possible, but the nanoplankton bloom appeared during

1973 and cell numbers remained relatively high all summer so that although many investigators (Biernacka 1948, Gilbricht 1954, Posta 1963, Zeitzschel 1967) consider temperature to be the controlling factor in tintinnid distribution, the exact mode of the temperature influence is still not at all clear.

Although tintinnids may experience minor maxima during periods of abundant dinoflagellates (as in Sept-Oct 1975), they are never numerous during diatom maxima and tintinnids are most abundant when only nanoplankters dominate the phytoplankton. This situation appears to hold true for the Scotian Shelf as well. However, Gold (personal communication) finds blooms of Tintinnopsis tubulosoides in January off Coney Island accompanied by large numbers of Skeletonema costatum, and Zeitzschel (1967) reported tintinnid maxima during diatom and dinoflagellate maxima in the North Atlantic. Certainly in culture large numbers of diatoms are detrimental to tintinnids, and they probably cannot feed on chain-forming diatoms. The true relationship between tintinnids and large phytoplankters may not be clear from Zeitzschel's data because of infrequent sampling. Skeletonema is often found in very short chains and even as single cells so they may thus be quite small and perhaps serve as a food source for this Tintinnopsis species.

The nanoplankton of the NWA consists primarily of phytoflagellates such as the following: the prasinophytes Pyramimonas and Tetraselmis; the haptophytes Chrysochromulina and Isochrysis; the unarmoured dinoflagellates Gymnodinium and

Glenodinium; the cryptophyte Rhodomonas (the most ubiquitous and abundant species); the craspedophyte Salpingoeca; the chrysophytes Dinobryon, Kephyrion and Pseudopedinella; and a small naviculoid diatom. The preponderence of phytoflagellates in the nanoplankton disagrees sharply with what was found by, for example, Yentsch and Ryther (1958) who stated that the nanoplankton consists almost exclusively of small diatoms and that their numbers are relatively constant (at least from March until July). However, their cell numbers are very low indeed and the discrepancy between their <60 μ fraction chlorophyll graph and their <60 μ fraction cell counts makes it fairly obvious that large numbers of phytoflagellates were probably destroyed by the formalin preservation of the samples.

Perhaps the most striking feature of tintinnid distribution (and other protozoan distribution as well) with time in the NWA is the rapidity with which they can appear and disappear. For example, on three successive days, the concentration of: (a) Euplotes sexcostatus went from 2175/l to 2900 to 215; (b) Helicostomella subulata went from 12,502/l to 44,040 to 7558; (c) Cyclotrichium meunieri went from 14,955/l to 34,824 to 1718; (d) Strombidium sulcatum went from 12,786/l to 165,930 to 2927. The reasons for this are unclear but it is a common phenomenon. As early as 1934 Lackey's data showed this erratic distribution in the water around Woods Hole. Vitiello's weekly samples (Nov 1962-May

1963) in the Bay of Algiers clearly showed this phenomenon as did Zeitzschel's (1967) monthly samples from the North Atlantic. Beers and Stewart (1970) also commented on how rapidly the tintinnids appear, reach a maximum and disappear. Mulford (1972) and Hedin (1974) showed very much less erratic curves for tintinnid abundance in Chesapeake Bay and a Swedish fjord respectively, but their relatively infrequent sampling intervals (monthly) could account for this. It is clear from my data (see Fig. 3 and Appendix A, Figs. 13 and 17, for example) that decreasing the sampling interval from two weeks to one week to one day only emphasizes the possible extremes of abundance.

Such "boom and bust" cycles also occur in cultures (Fig. 31; Appendix D, Figs. 1-3) but they are not quite as extreme. However, a most spectacular crash cycle occurred in January 1975 in Dalhousie University's Tower Tank (3 m in diameter, 10 m deep). The tank was filled with unfiltered sea water from the NWA on 15 Jan and left undisturbed. A tintinnid bloom was first noticed on 23 Jan. On 25 Jan the dominant species was Tintinnopsis karajacensis followed by Helicostomella subulata followed by Tintinnopsis strigosa. One day later T. karajacensis was still the dominant species (2.36×10^6/l) but T. strigosa (1.13×10^6/l) was more abundant than H. subulata (2.1×10^5/l) in the tank's surface waters. Note the rapidity with which the bloom developed (8 days) and the rapidity with which species dominance changed (1 day). On

28 Jan there was not one tintinnid to be found in the tank. However, I noticed that by this time there were also no suitable food organisms for the tintinnids in the tank and that the tank was abundantly populated by copepods. It is my belief that the primary cause of the tintinnid demise in the tank (and probably true for natural populations as well) was exhaustion of food supply accompanied by heavy predation upon them by copepods or other macrozooplankton. Tintinnid decline in culture is more probably due to adverse effects of metabolic wastes and bacterial overgrowth.

It is difficult to assess the effect of predation as a controlling influence on tintinnid populations as no data are available on the kinds and distribution of possible predators in the NWA. But macrozooplankton are known to consume them. Harding (1972) found loricae in the gut of large, deep-water copepods. Zeitzschel (1967) reported over 4000 Parafavella loricae in one Meganictiphanes gut. I have seen Tintinnopsis loricae in the gut of the Mytilus. Smaller copepods may consume tintinnids in the same manner as they consume large diatoms; i.e., they break them apart and suck out the insides. Hence, small copepods may consume tintinnids but not their loricae.

The rate at which tintinnids reproduce no doubt has some effect on their abundance. Such rate data are scarce. Gold (1970, 1971) reported a doubling time of one day for Metacylis and 2.5-6 days for Tintinnopsis beroidea cultures. My cultures of Helicostomella and two species of Tintinnopsis had doubling

times of 3-5 days. However, reproduction at the rates observed in these cultures cannot account for some of the increases that have been observed in nature. Conversely, the cultures invariably decline rapidly after they reach their peak, but the rate of decline also is less rapid than the observed decrease in natural populations. Various hypotheses have been advanced in an attempt to explain this variability. None of these can be regarded as firmly founded, and they are not mutually exclusive. However, they deserve to be reviewed briefly:

1. Prey-predator relations. Under conditions of optimal food supply the rate of growth may in fact be greater than is indicated by culture experiments. Short term feeding experiments described in a later section indicate a highly variable feeding rate which in some cases is large enough to suggest that the maximum ingestion rate could support a doubling rate of considerably less than one day. In nature the food supply is patchy. An intense localisation of food organisms might give rise to particularly favourable conditions for a burst of protozoan growth, which in turn would use up the food supply quickly. Blackbourn (1974) concluded that large species such as Tintinnopsis subacuta eat at a sufficient rate and are numerous enough at times to decimate the nanoplankton in a day's time and induce a population crash. Predation by zooplankton would accentuate the decline. In general the population crashes observed in nature seem more understandable than the very rapid increases.

2. Vertical movement and swarming. The tendency for species to swarm at particular depths has been noted. The position in the vertical column may be variable. Vitiello (1964) stressed currents, insolation and cloud cover as agents causing the appearance and disappearance of tintinnids in surface waters. Diel vertical migration has been noted in the NWA and will be still more obvious in a later discussion of the Scotian Shelf. In an ordinary sampling scheme, variability due to these movements cannot be distinguished accurately from changes in overall population size and may have been responsible for some of the apparent increases and decreases.

3. Relations with physical variables. Gold (1973b) suggested that salinity may affect species dominance but his experiments invovled salinity differences of 13 $^{o}/_{oo}$. Such salinity differences do not occur in the NWA, even in the surface waters, nor do such changes occur in the open ocean. Vitiello (1964) also rejected salinity as a controlling factor in the open ocean.

The possible effect of temperature on the abundance of tintinnids has already been mentioned. Another possible influence may be the tides or seiches in the NWA. An attempt to study tide and seiche influence was made on 15 July 1975. Samples were taken every half hour from 0530 until 2030 (every 10 minutes from 1300 until 1700), settled and counted. The seiche has a period of about 30 minutes and has no effect on

either Helicostomella subulata or Tintinnopsis parvula. Nor did the daily tide (low tide: 0900; high tide: 1500) appear to have an effect (Fig. 13). However, these data indicate a rise to the surface (especially T. parvula) at dawn and dusk but since I made daily collections only during daytime low tide, this effect on my results would be minimal (except that the daily samples probably represent minimum abundances since they were all taken from the surface). Indeed, a plot of time of sampling vs. abundance of Helicostomella (Appendix A, Fig. 18) shows no correlation. On the other hand, a plot of daily tidal range vs. Helicostomella in the same figure appears to show that abundance maxima occur about one week before the period of the major maximum tidal range. This relationship might be fortuitous and indeed is only marginally valid statistically. But consider the following: The spring tidal cycle has a period of about 28 days. Fourier analysis shows (Figs. 14 and 15) that: (a) Helicostomella abundance exhibits a cycle of about 30 days; (b) Cyclotrichium, a cycle of about 27 days; (c) S. calkinsi, about 30 days; (d) S. strobilus, about 30 days.

The implications of these results are problematical. There is some evidence to support the idea that tides can provide a physical forcing mechanism which tends to create plankton patchiness, but probably not in the context of the low frequencies which appear to be important here. If tidal variations significantly affect exchange rates with the open sea there could be a pulsating rate of nutrient supply which

Figure 13. Effect of daily tidal range on the abundance of Tintinnopsis parvula and Helicostomella subulata: 15 July 1975

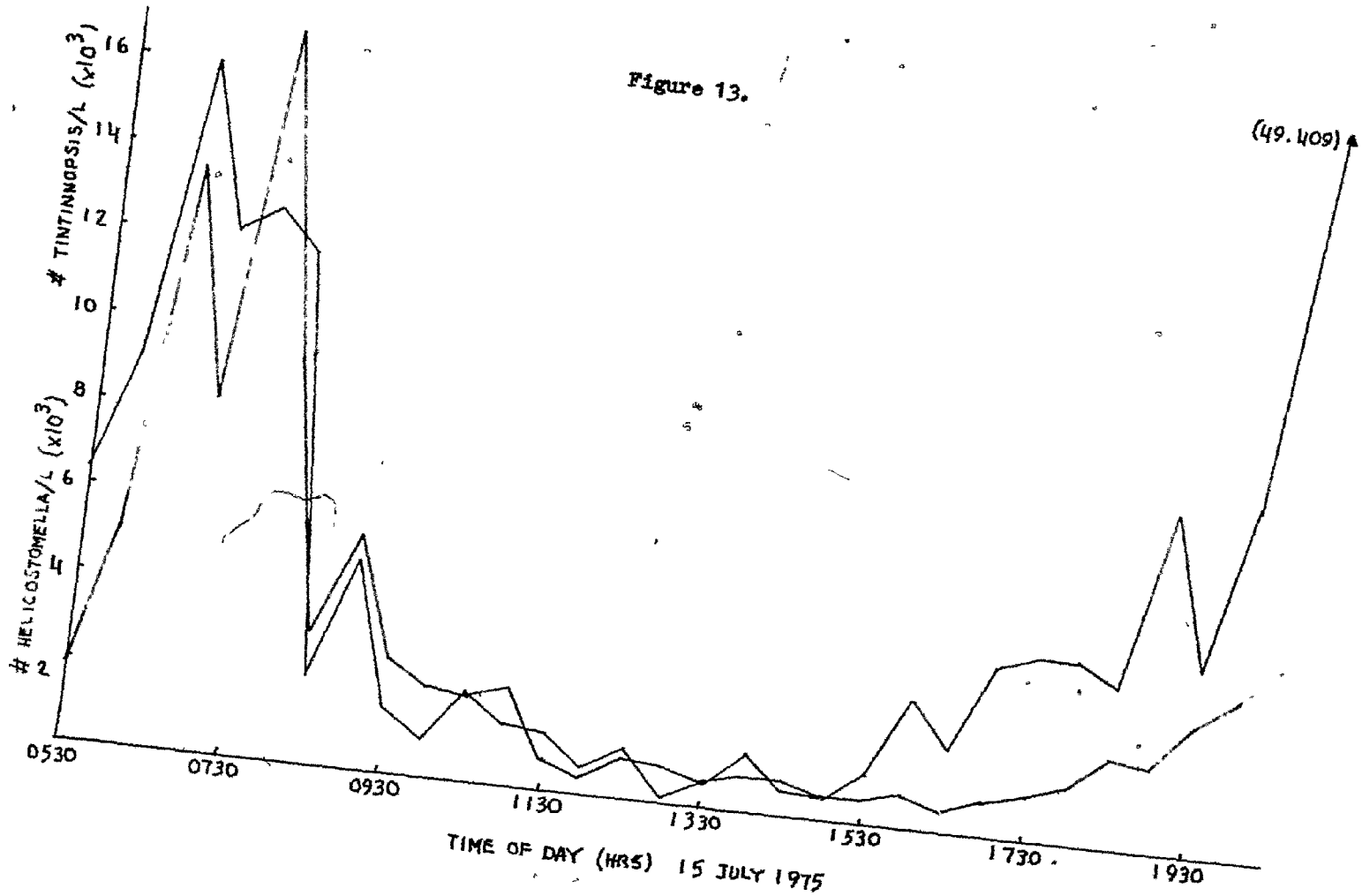
Figure 14a. Fourier analysis of log abundance of Helicostomella subulata: 15 June - 12 October 1975 (120 days)

Figure 14b. Fourier analysis of log abundance of Cyclotrichium meunieri: 23 May - 10 August 1975 (80 days)

Figure 15a. Fourier analysis of log abundance of Strombidium calkinsi: 13 April - 10 August 1975 (120 days)

Figure 15b. Fourier analysis of log abundance of Strombidium strobilus: 12 May - 9 August 1975 (90 days)

Figure 13.


TINTINNOPSIS/L (x10^3)
HELICOSTOMELLA/L (x10^3)
16
14
12
10
8
6
4
2
(49.409)
0530
0730
0930
1130
1330
1530
1730
1930
TIME OF DAY (HRS) 15 JULY 1975

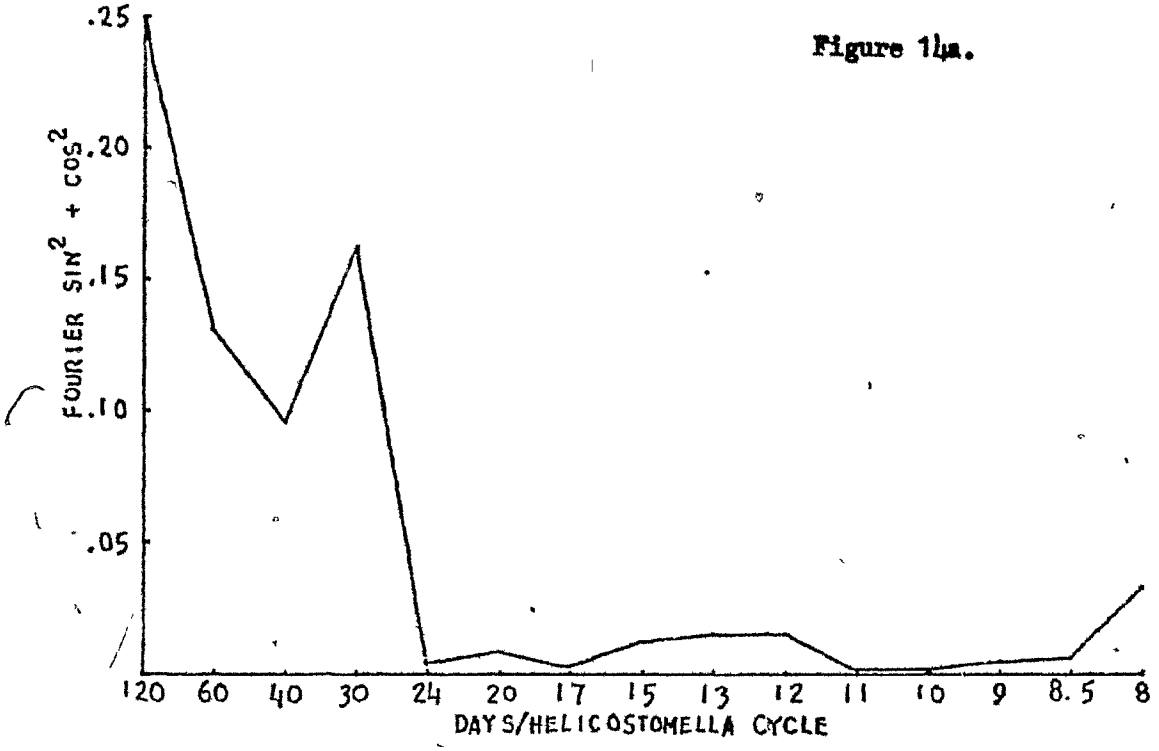


Figure 14a.

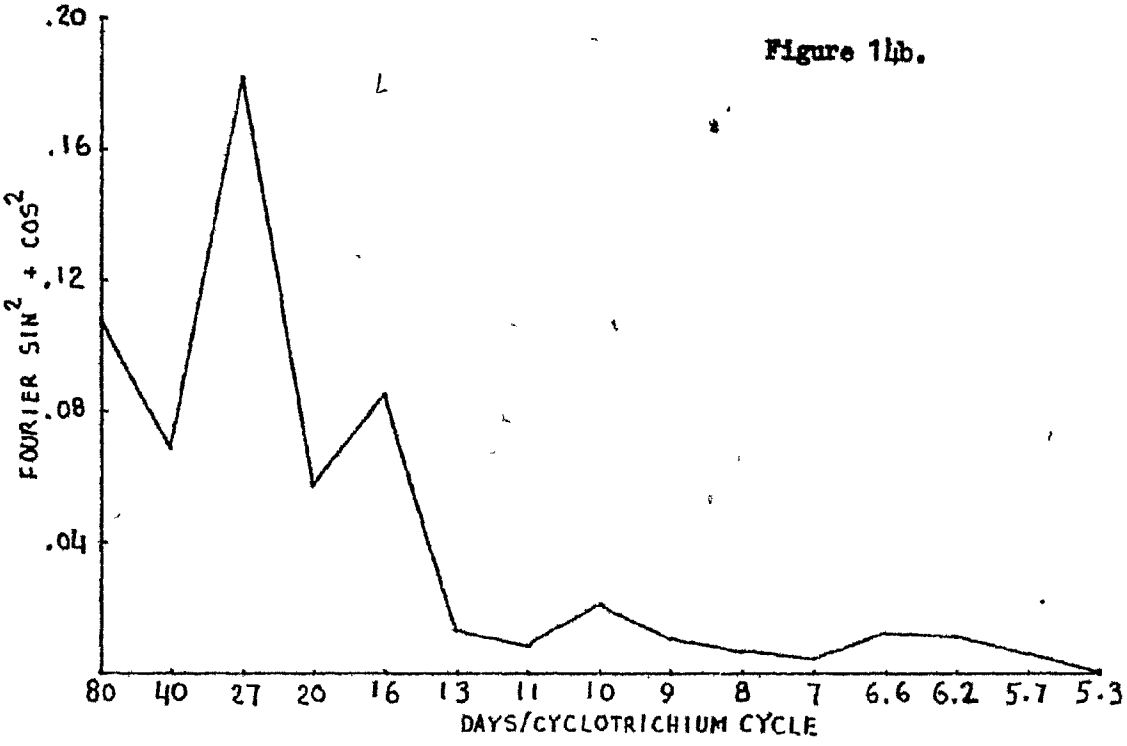


Figure 14b.

Figure 15a.

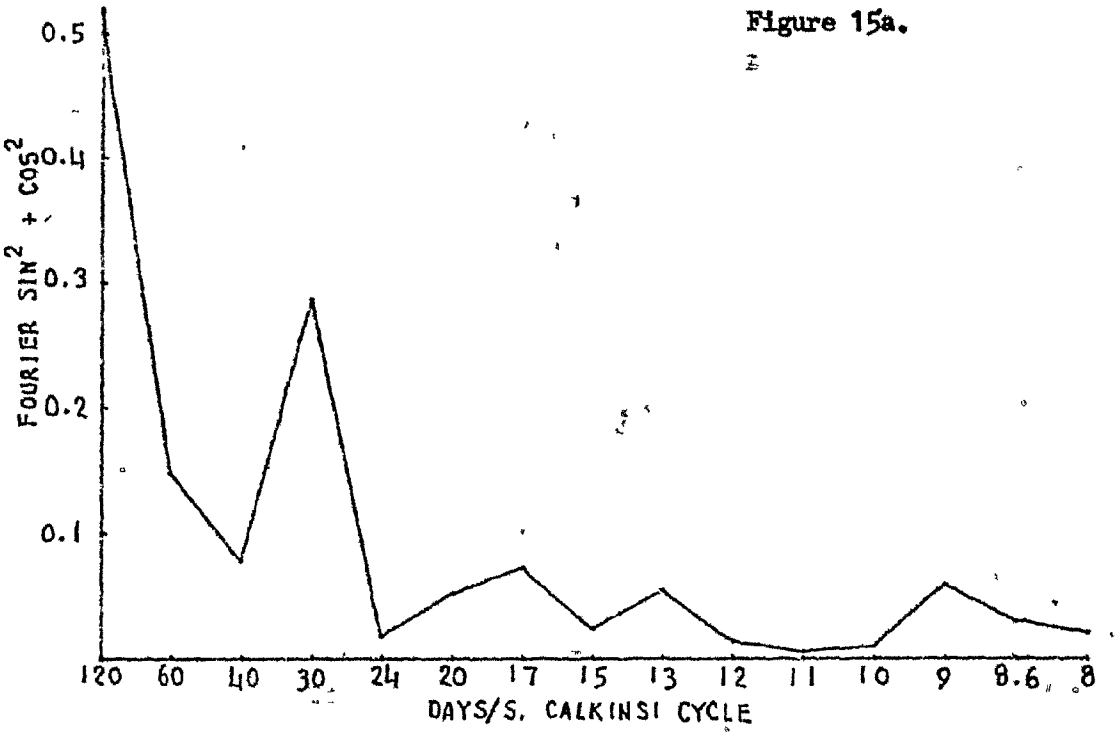
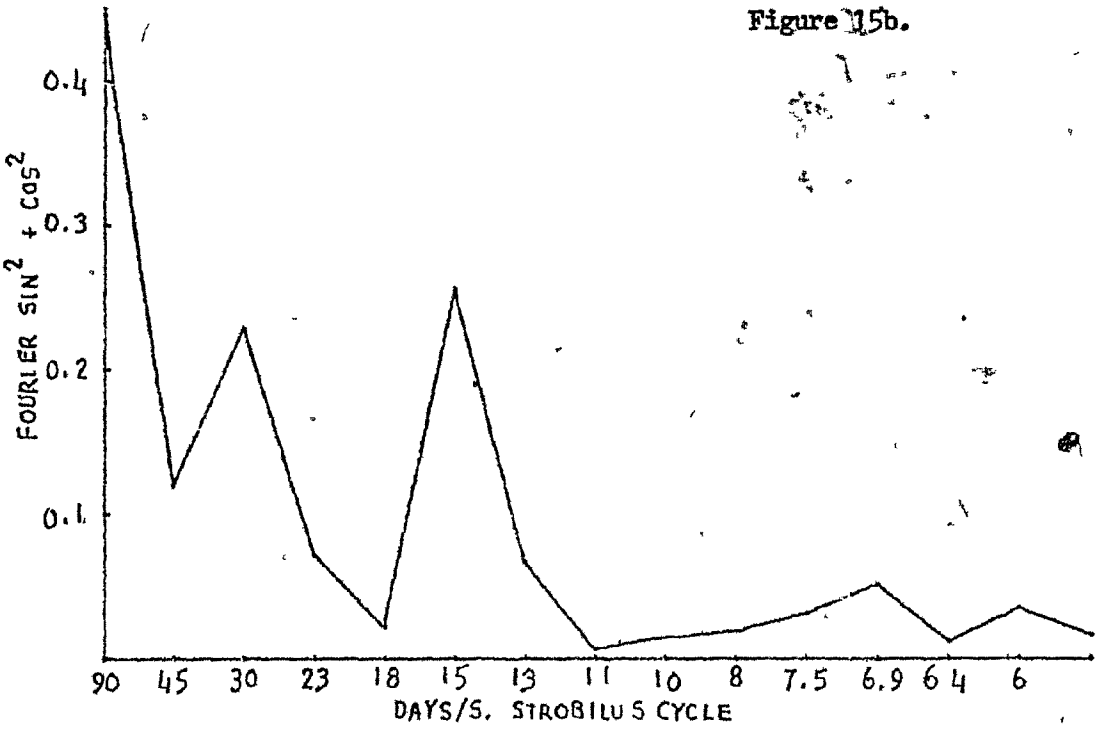


Figure 15b.



could carry over into secondary productivity, but this is completely speculatory.

Some of the other species exhibit cycles as well. Fourier analysis for T. paivula during 1 June-9 Aug 1975 exhibits similar peaks to the temperature analysis during the same period at 10 and 14 days (Fig. 16). Euplotes exhibits 9 and 20 day cycles; Strombidium sp., 40 days; S. conicum, 25 days; S. sulcatum, 42 days. These results are even more inexplicable. The discussion is getting into a new realm of biological oceanography that has been inadequately explored and is ill understood. With the gradual development of methods for continuous underway sampling (fluorometers, zooplankton counters) we are beginning to acquire descriptive information about plankton patchiness in general. However, the interpretation of the results in relation to physical and biological causative factors is still in a formative state. The difficulties of detailed studies of tintinnid distribution are insurmountable at present, and the present discussion can do no more than point out problems for future study.

SUMMARY

Tintinnids and other protozoa in the NWA occur primarily in late summer and early fall, during which time they and the nanoplankton on which they probably feed are practically the only microplankton in the water column. The animals' presence is marked by huge variations in abundance over short periods of time (less than one day) and one species may re-

Figure 16a. Fourier analysis of log abundance of Tintinnopsis parvula: 1 June - 9 August 1975 (70 days)

Figure 16b. Fourier analysis of NWA surface temperature: 1 June - 9 August 1975 (70 days)

Figure 16a.

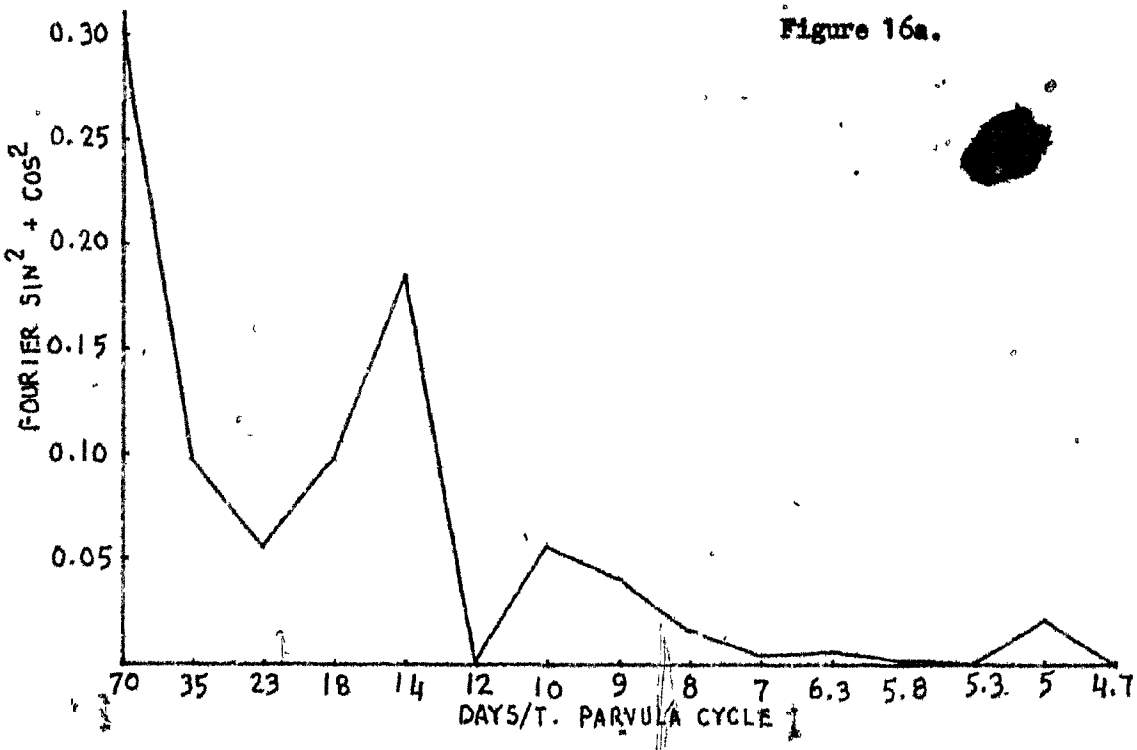
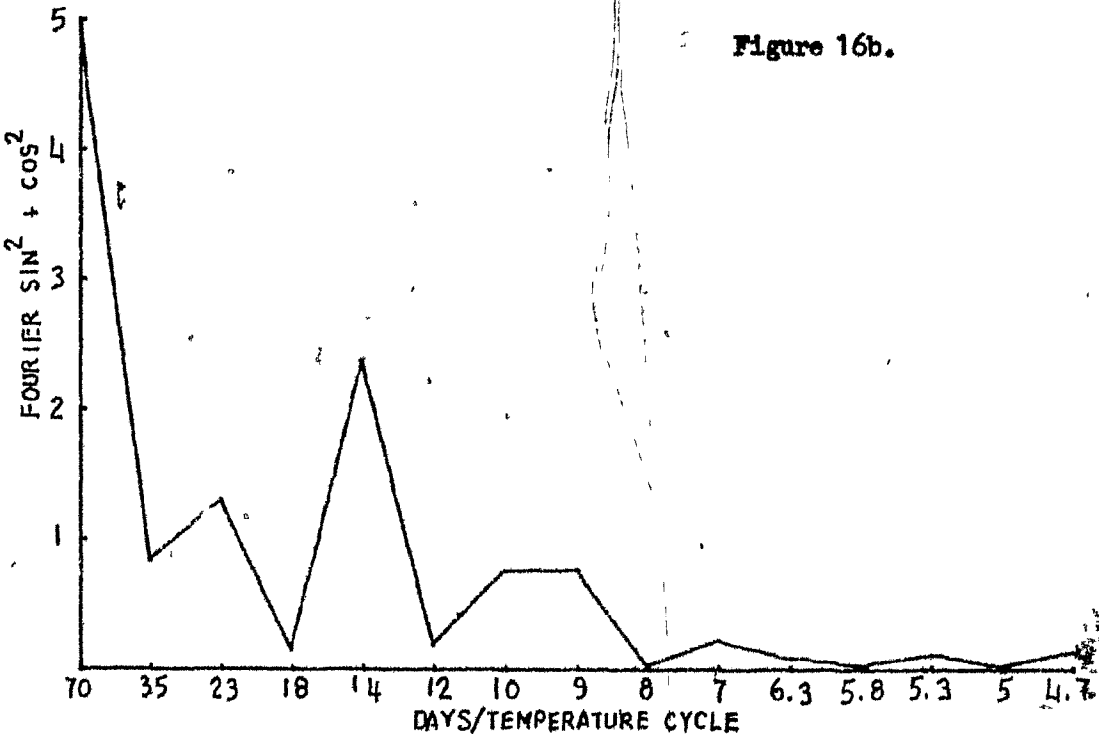


Figure 16b.



place another with great rapidity (less than one week). The control of tintinnid populations is most probably food supply modified by complex interactions with grazers, temperature, reproductive rates and perhaps even weather and the tides.

3. PROTOZOAN ABUNDANCE AND DISTRIBUTION ON THE SCOTIAN SHELF

INTRODUCTION

Dalhousie University Department of Oceanography is actively working on a transect of seven stations lying perpendicularly to the Atlantic coast of Nova Scotia directly off Halifax (Fig. 17). The main interest of this investigation centers on primary production and the nutrient cycle in this area.

It has long been known that zooplankton excretion contributes to the nutrient requirements of the phytoplankton. Fournier and his colleagues (personal communication) have determined the excretion rates of the Scotian Shelf macrozooplankton. However, nothing is known of the contribution of protozoa to the nutrient pool in offshore waters. In fact, little is known of the protozoa in this area at all. Wright (1907) presented a taxonomic description of the protozoa and other plankton in the Strait of Canso and Gaarder (1946) published taxonomic data for the Newfoundland Banks. There are also some early papers dealing semi-quantitatively with the protozoa and other plankton in the Gulf of Maine and in the Bay of Fundy (Bigelow 1924, Bigelow, Lillick and Sears 1940, Gran 1933, Gran and Braarud 1935).

Before any attempt at the determination of the contribution of the protozoa to the nutrient cycle of the Scotian

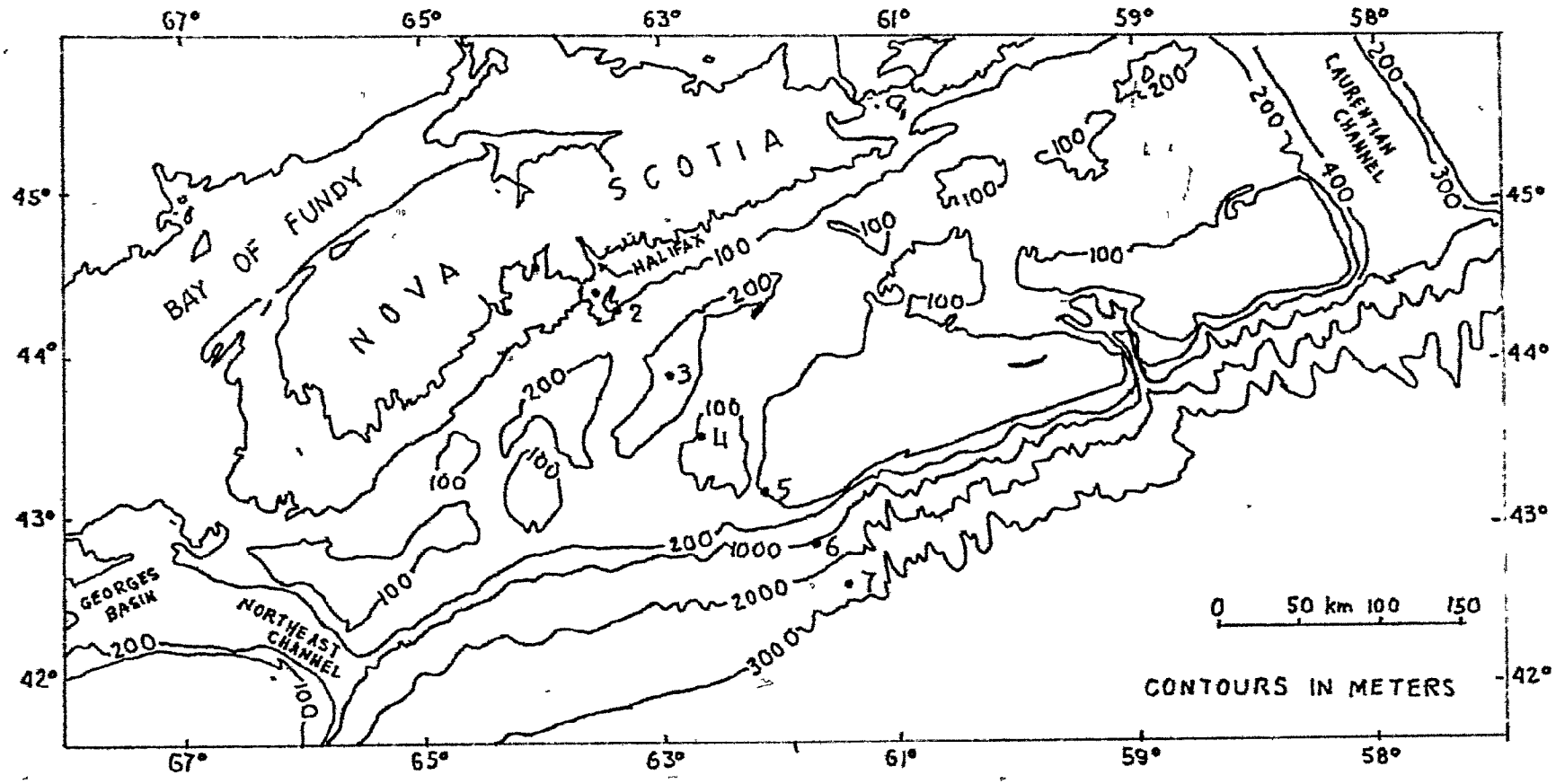


Figure 17. Scotian Shelf transect station locations.

Shelf can be pursued, it is necessary to determine the distribution and abundance of this group of microorganisms in that area. The need for this information prompted the present study of the Scotian Shelf protozoa.

METHODS

Collections were made during four cruises along the Scotian Shelf (SS) transect. Figure 17 shows the locations of the seven stations. Table 4 lists station latitudes, longitudes and water depths. The cruises took place during the following periods:

SS I: 29 May - 3 June 1974
SS II: 4 - 8 November 1974
SSIII: 4 - 6 March 1975
SS IV: 25 - 29 August 1975

500-ml samples were collection using 12-l Niskin bottles (and preserved with 1% basic Lugol's) from various depths (usually 0, 10, 25, 50 and 75 m, and sometimes from 100, 150, 200 and 250 m). For the enumeration of the protozoa, 400 ml of the preserved sea water sample were settled out and counts were made at 200x using a Wild M-40 microscope.

RESULTS

Eighty species of protozoa were identified from the four Scotian Shelf cruise samples, 65 of which were ciliates, 48 being tintinnids and 8 being strombidia. Eight radiolarian species were found. Table 5 lists all species identified as well as their stations of occurrence. Table 6 also lists the

Table 4. Scotian Shelf transect station locations.

STATION	LATITUDE (N)	LONGITUDE (W)	DEPTH (m)
1	44°24'	63°28'	75
2	44°16'	63°19'	150
3	43°53'	62°53'	280
4	43°29'	62°27'	80
5	43°11'	62°06'	100
6	42°51'	62°44'	1000
7	42°32'	61°24'	2500

species along with their months of occurrence. Table 7 presents some general statistics of the four cruises. Appendix C, Table 1 lists the species along with information concerning their maximum abundances during each of the four cruises. Appendix C, Tables 2, 3 and 4 summarize the total number of protozoa/l, the total number of species found and the species diversity indices, respectively, for each station and depth during each of the cruises. Appendix C, Tables 5 and 6 average the above data for the top 50 m of the water column and for the 50 - 250 m layer respectively.

As was the case for the North West Arm (NWA), protozoa were most abundant during summer (August) and fall (November). Tintinnids were particularly scarce during March and June (except at the outer two stations during June), which was also true of the NWA. The strombidia, on the other hand, were comparatively abundant at all stations and times although they

Table 5. Scotian Shelf protozoa and their stations of occurrence

SPECIES	STATION NUMBER 1	2	3	4	5	6	7
Phylum PROTOZOA							
Subphylum PLASMODROMA							
Class SARCODINA							
Subclass RHIZOPODA							
Order TESTACIDA							
Difflugia oblonga		x	x		x		
Euglypha laevis	x			x	x		x
Order FORAMINIFERIDA							
Candeina nitida					x		
Globigerina bulloides			x	x			x
Subclass ACTINOPODA							
Order RADIOLARIDA							
Astrosphaera hexagonalis			x				
Coelacantha dogiella			x				
Coelodendrum furcatissima				x			
Lithomelissa setosa		x	x	x	x	x	x
Phormacantha hystrix			x				
Sticholonche zanclea	x	x	x			x	x
Triplagia primordialis		x	x				x
Xiphosphaera vesta			x				
Subphylum CILIOPHORA							
Class CILIATA							
Subclass HOLOTRICHIDA							
Order BYMNOSTOMATIDA							
Cyclotrichium meunieri	x	x	x	x	x	x	x
Didinium nasutum	x			x	x	x	x
Lacrymaria alor		x	x	x			
Mesodinium pulex	x	x	x	x	x		x
Mesodinium rubrum	x	x	x		x	x	x
Tiarina fusus	x	x	x	x	x	x	x
Order HYMENOSTOMATIDA							
Frontonia marina		x	x	x	x	x	x
Subclass SPIROTRICHA							
Order OLIGOTRICHIDA							
Strombidium sp.	x	x	x	x	x	x	x
Strombidium acuminatum			x	x	x	x	
Strombidium cornucopiae				x			
Strombidium conicum	x	x	x	x	x	x	x
Strombidium ovale	x	x	x	x	x	x	x
Strombidium strobilus	x	x	x	x	x	x	x
Strombidium sulcatum	x	x	x	x	x	x	x
Strombidium typicum		x	x		x	x	x
Tontonia gracillima	x	x	x	x	x	x	x
Order TINTINNIDA							

Table 5. (continued)

SPECIES	STATION NUMBER 1	2	3	4	5	6	7
Acanthostomella conicoides	x	x	x		x		x
Acanthostomella norvegica	x	x	x	x	x	x	x
Amphorella gaarderae							x
Amphorella quadrilineata	x	x	x	x	x	x	x
Ascampbella urceolata							x
Climacocylis scalaroides					x		
Codonella acuta	x	x	x	x	x		x
Codonellopsis contracta						x	x
Dadayiella bulbosa			x		x		x
Dictyocysta elegans					x		
Dictyocysta reticulata							x
Dictyocysta speciosa					x	x	x
Epiplocylis aguminata					x		x
Eutintinnus fraknoi							x
Favella franciscana						x	
Helicostomella subulata		x		x	x		
Metacylis corbula	x	x	x	x	x	x	x
Parafavella edentata	x				x	x	x
Parafavella gigantea	x	x	x			x	
Parafavella parumdentata	x	x	x	x	x	x	x
Parundella grandis							x
Parundella major						x	x
Parundella minor		x					x
Parundella subcaudata							x
Poroecus curtis							x
Proplectella globosa	x	x	x		x		x
Proplectella parva					x		x
Proplectella perpusilla				x			
Proplectella subacuta					x		
Proplectella subcaudata							x
Proplectella tumida	x		x				
Protorhabdonella curta			x	x	x	x	x
Ptychocylis drygalskii	x		x	x		x	
Ptychocylis minor							x
Salpingella accuminata			x			x	x
Salpingella curta							x
Salpingella gracilis		x					x
Stenosemella ventricosa	x	x	x		x		x
Tintinnopsis cylindrica							x
Tintinnopsis lata	x	x	x	x	x	x	x
Tintinnopsis parvula	x	x					
Tintinnopsis pistilum				x			
Tintinnopsis sacculus	x				x		
Tintinnopsis strigosa			x				

Table 5. (continued)

SPECIES	STATION NUMBER 1	2	3	4	5	6	7
Tintinnopsis undella	x	x	x	x		x	x
Tintinnus tubulosus	x	x	x		x	x	x
Undella columbiana		x	x		x	x	x
Undellopsis pacifica	x	x				x	x
Order HYPOTRICHIDA							
Euplotes sexcostatus	x	x					
Class SUCTORIA							
Order SUCTORIDA							
Trichophyra columbiae					x		

too reached their peak abundance during August and declined greatly during November. It should be noted that neither the tintinnids nor the strombidia on the Scotian Shelf attained the great abundances that were found in the NWA.

Figures 18 and 19 are histograms presenting the percentage of the total protozoa comprising tintinnids and strombidia, respectively, in all samples from the Scotian Shelf. Tintinnids commonly comprised less than 50% (93% of the time, in fact) of the total protozoa while the strombidia commonly comprised more than 50% (80% of the time). Margalef (1963) found much the same pattern among the protozoa of the Mediterranean Sea; i.e., more than 90% of the ciliates there were oligotrichs while only about 5% were tintinnids. The pattern was repeated for tintinnids in the NWA as well; i.e., they comprised 10% or less of the total protozoan population 52% of the time. On the other hand, the strombidia comprised less than 50% of the total protozoa of the NWA 55% of the time

Table 6. Scotian Shelf protozoa and their months of occurrence

SPECIES	MARCH (SSIII)	JUNE (SSI)	AUGUST (SSIV)	NOVEMBER (SSII)
Difflugia oblonga			x	x
Duglypha laevis	x		x	x
Candeina nitida		x		
Globigerina bulloides	x		x	x
Astrosphaera hexagonalis			x	x
Coelacantha dogiella				x
Coelodenorum furcatissima				x
Lithomelissa setosa	x	x	x	x
Phormacantha hystrix				x
Sticholonche zanclea	x	x	x	x
Triplagia primordialis			x	x
Xiphosphaera vesta			x	
Cyclotrichium meunieri	x	x	x	x
Didinium nasutum	x		x	x
Lacrymaria alor				x
Mesodinium pulex			x	x
Mesodinium rubrum			x	x
Tiarina fusus	x		x	x
Frontonia marina	x		x	x
Strombidium sp.	x	x	x	x
Strombidium acuminatum	x	x	x	x
Strombidium cornucopiae				x
Strombidium conicum	x	x	x	x
Strombidium ovale	x	x	x	x
Strombidium strobilus	x	x	x	x
Strombidium sulcatum	x	x	x	x
Strombidium typicum			x	x
Tontonia gracillima	x	x	x	x
Acanthostomella conicoides			x	x
Acanthostomella norvegica	x	x	x	x
Amphorella gaarderae			x	
Amphorella quadrilineata	x	x	x	x
Ascampbella urceolata		x		
Climacocylis scalaroides			x	
Codonella acuta				x
Codonellopsis contracta	x	x		
Dadayiella bulbosa			x	
Dictyocysta elegans				x
Dictyocysta reticulata			x	
Dictyocysta speciosa		x		
Epiplocylis acuminata			x	
Eutintinnus fraknoi			x	
Favella franciscana		x		
Helicostomella subulata		x	x	

Table 6. (continued)

SPECIES	MARCH (SSIII)	JUNE (SSI)	AUGUST (SSIV)	NOVEMBER (SSII)
Metacylis corbula		x		x
Parafavella edentata	x		x	
Parafavella gigantea	x		x	x
Parafavella parumdentata	x	x		x
Parundella grandis			x	
Parundella major	x	x	x	
Parundella minor		x		
Parundella subcaudata			x	
Poroecus curtis	x			
Proplectella globosa			x	
Proplectella parva		x		
Proplectella Perpusilla				x
Proplectella subacuta	x	x		
Proplectella subcaudata			x	
Proplectella tumida	x			x
Protorhabdonella curta	x	x	x	x
Ptychocylis drygalskii	x	x		x
Ptychocylis minor	x			
Salpingella accuminata		x		
Salpingella curta		x		
Salpingella gracilis			x	
Stenosemella ventricosa			x	
Tintinnopsis cylindrica			x	
Tintinnopsis lata		x		x
Tintinnopsis parvula	x			
Tintinnopsis pistilum				x
Tintinnopsis sacculus		x	x	
Tintinnopsis strigosa				x
Tintinnopsis undella		x		x
Tintinnus tubulosus		x	x	x
Undella columbiana			x	x
Undellopsis pacifica		x		
Euplotes sexcostatus	x			
Tricophyra columbiae			x	

and more than 50% of the total 45% of the time. The reduced proportion of the strombidia in the NWA was due in part to the occasional high abundance of Cyclotrichium meunieri there. This latter species is rather uncommon on the Scotian Shelf. These data emphasize the need for further knowledge of the

Table 7. General summary of the data

	MAR-SSIII			JUNE-SSI			AUG-SSIV			NOV-SSII		
	#	ST	Z(m)	#	ST	Z(m)	#	ST	Z(m)	#	ST	Z(m)
Total # samples	43			47			50			47		
# protozoan species	31			34			49			45		
# tintinnid species	14			22			25			18		
Max. # protozoa/l	1503	4	0	3490	2	0	16527	5	30	5335	7	1
	1503	6	10									
Min. # protozoa/l	65	3	100	36	3	0	92	7	250	18	3	200
Max. # species	10	2	0	14	7	2.5	22	7	3.5	13	2	0
	10	2	10	14	7	200				13	3	0
	10	2	25									
	10	3	0									
	10	7	0									
Min. # species	2	6	200	2	2	100	5	3	150	1	3	200
				2	3	0	5	3	250			
							5	7	250			
Max. species diversity	2.01	3	23	2.42	7	200	2.28	7	3.5	2.28	1	50
Min. species diversity	0.69	6	200	0.39	3	42	1.04	3	25	0.00	3	200
Max. # tintinnids/l	67	6	10	1039	7	50	4054	1	0	1289	3	0
	67	6	25									
	67	6	50									
Min. # tintinnids/l	0	2	75	0	1	12	0	3	250	0	3	200
	0	2	100	0	2	0	0	7	200	0	4	50
	0	4	10	0	2	25				0	4	75
	0	5	44	0	2	75				0	5	10
	0	6	200	0	2	100						
	0	7	19	0	3	0						
				0	3	75						
				0	3	21						
				0	4	0						
				0	4	24						
				0	4	70						
				0	5	0						
				0	5	21						
Max. # strombidia/l	1289	4	0	3132	2	0	15144	5	30	3777	4	0
	1289	6	0									
	1289	6	10									
Min. # strombidia/l	13	6	200	18	6	75	26	7	250	0	3	150
				18	6	100						
Max. % tintinnids	36	6	150	75	6	100	26	1	0	100	3	150
Min. % tintinnids	0			0			0			0		
Max. % strombidia	92	6	50	100	2	100	94	1	25	100	3	200
										100	4	75
Min. % strombidia	5	1	50	13	6	100	28	7	250	0	3	150
										0	4	50

Figure 18.

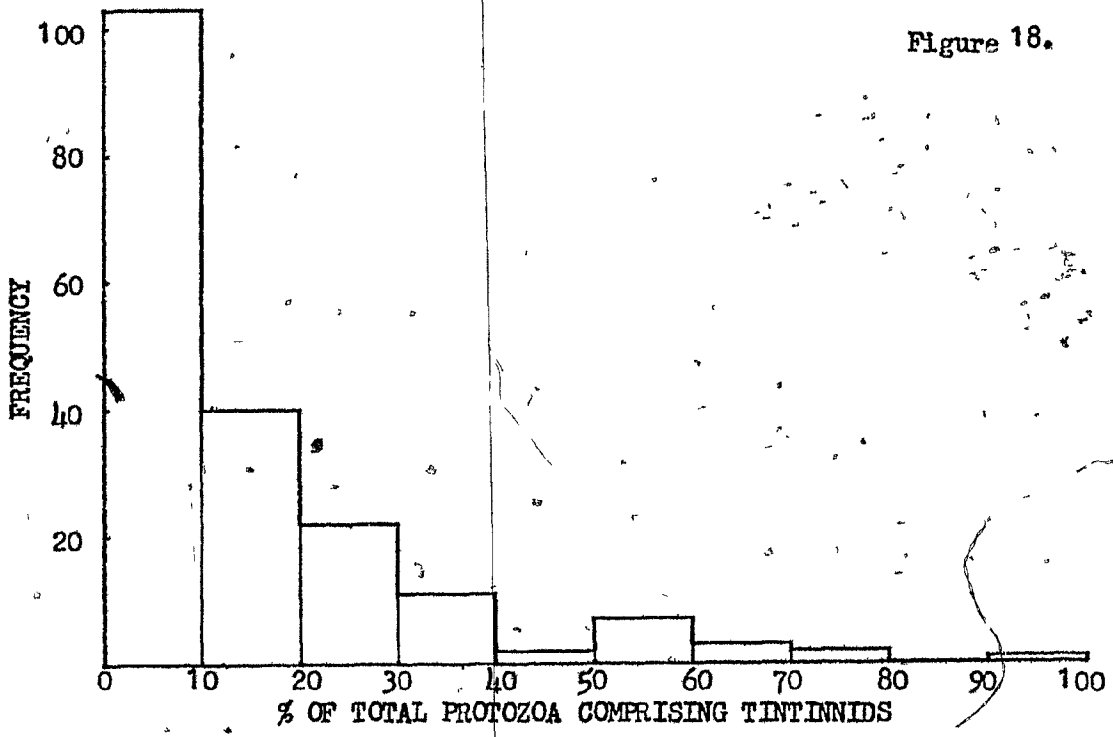
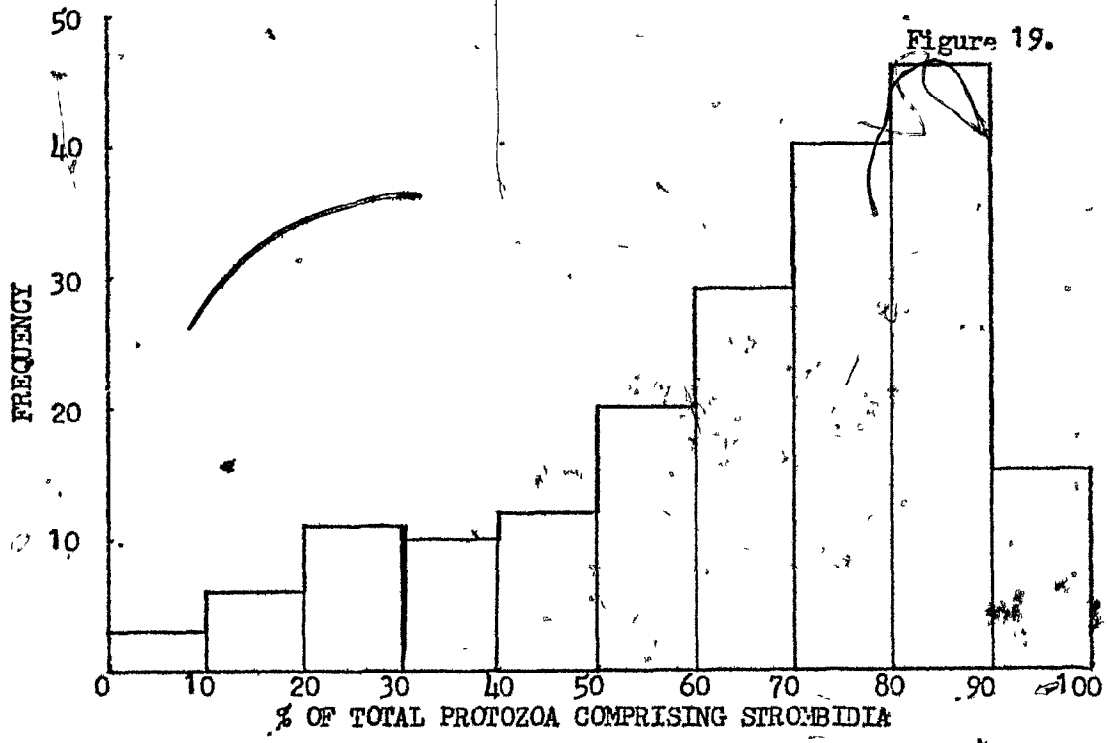


Figure 19.



distribution, abundance and role of strombidia in marine waters.

Both tintinnids and strombidia were more abundant in the top 50 m of the water column than in the 50 - 250 m layer. However, the tintinnids generally comprised a greater proportion of the total protozoa in deeper water than in the surface layer. The proportion of strombidia was slightly lower in deeper water.

During the March cruise at Stations 2, 3 and 5 and during November at Station 3 hydrocasts were made around midnight and noon. At Stations 2 and 3 in March there were substantially more protozoa at the surface at night than during the day. Table 8 lists these diurnal differences in protozoan abundance. The differences were due primarily to the number

Table 8. Diurnal variation in protozoa abundance in surface water

	NOON	MIDNIGHT
STATION 2		
Total number of protozoa	698	3490
Number of Strombidium conicum	125	1396
Number of Strombidium sulcatum	72	1002
Number of Strombidium sp.	179	591
STATION 3		
Total number of protozoa	36	1505
Number of Strombidium conicum	0	304
Number of Strombidium sulcatum	0	430
Number of Strombidium sp.	18	412

of strombidia at the surface. There seemed to be no difference in the tintinnid population but tintinnids were not very abundant during March. On the other hand, at Station 5 during

March and at Station 3 during November there was little difference between day and night samples either among the tintinnids, the strombidia or total protozoa. In the previous section I pointed out that Helicostomella subulata and Tintinnopsis parvula appeared to undergo diurnal vertical migration in the NWA. Zaika and Ostrovskaya (1972) reported vertical migration for four unnamed tintinnids and two strombidia in the Mediterranean Sea. Vitiello (1964) also reported vertical migration of up to 50 m for tintinnids in the Bay of Algiers. Zaika and Ostrovskaya (1972) pointed out, however, that protozoan vertical migration may occur only over short distances so that such migration on the Scotian Shelf might have been masked by the relatively large vertical distances separating the samples at Station 5 in March and Station 3 in November.

That large differences in abundance can occur over short depth intervals is revealed in Table 9.which presents data from the August cruise. Again, most of the variability is due to strombidia with minor variations in tintinnids.

Table 9. Total protozoan abundance variation with depth

STATION 3		STATION 5		STATION 7a		STATION 7b	
Z(m)	#p/l	Z(m)	#p/l	Z(m)	#p/l	Z(m)	#p/l
0	6403	0	8927	0	2806	0	5659
2.2	5718	4.5	7933	3.5	3127	4.5	4548
5	4590	10.5	10671	8	2416	10.5	3167
7.5	4818	15	10054	11	1918	15	1247
11.4	6599	23	7721	17	912	23	2279
15	2672	30	16527	22.5	980	30	10994
23	1303	50	1867	50	10124		
50	577	75	588	75	347		

In addition to variability in space there is also a great deal of variability in time. The samples from Station 7a and 7b above were collected a few hours before midnight on August 27 and 28 respectively. The 10,000+/l patch rose from 50 to 30 m and there were about twice as many protozoa on the 28th as on the 27th. A similar distribution was found at Station 4 during November (samples collected at midnight):

Depth (m)	Total number of protozoa/l	
	5 November	6 November
0	2183	4673
10	1470	2292
25	860	717
50	81	460

Again, the population seemed to have doubled within a 24-hour period.

Station 3 during November was particularly interesting:

Depth (m)	Total number of protozoa/l		
	4 Nov(1915hrs)	7 Nov(1145hrs)	8 Nov(0040hrs)
0	3760	1290	1075
10	1504	735	715
25	2310	860	216
50	949	287	162

The shapes of the November 4th and 7th abundance curves are the same (Fig. 23) although there were about three times as many protozoa on the 7th. Although the abundance of protozoa on November 7th and 8th were similar, the shapes of the distribution curves were quite different.

DISCUSSION

It is clear that tintinnids were more common inshore than offshore. The relatively greater number of tintinnids (and

indeed of other protozoa) at Stations 6 and 7 during June is a bit puzzling but a glance at the temperature structure at these stations (Figs. 20-23) makes it clear that this area was under the influence of a distinctly different water type and this may account for the large number of tintinnids.

Figures 20-23 show graphs of total number of protozoa (in red) superimposed on bathythermograph traces. There is no consistent trend in the abundance-temperature relationship. The only immediately obvious feature of these graphs is that maximum abundance occurred in the top 50 m. It is also obvious that both surface and subsurface maxima may occur, again with no consistent trend relative to station or time.

The observed variability in time and perhaps space may be explained by assuming that reproduction had occurred during the time between samples; and, indeed, a doubling time of one day is not unreasonable for strombidia and other protozoa. Still, such variability in time and space make the inadequacy of the sampling programme in both dimensions painfully obvious. On the other hand, the variability with time does not seem to be as severe as that encountered in the NWA protozoan populations.

Although a total of 80 protozoan species were identified on the Scotian Shelf there were never more than about half this number present during any one cruise (Table 7). More species were found in August and November than in March and

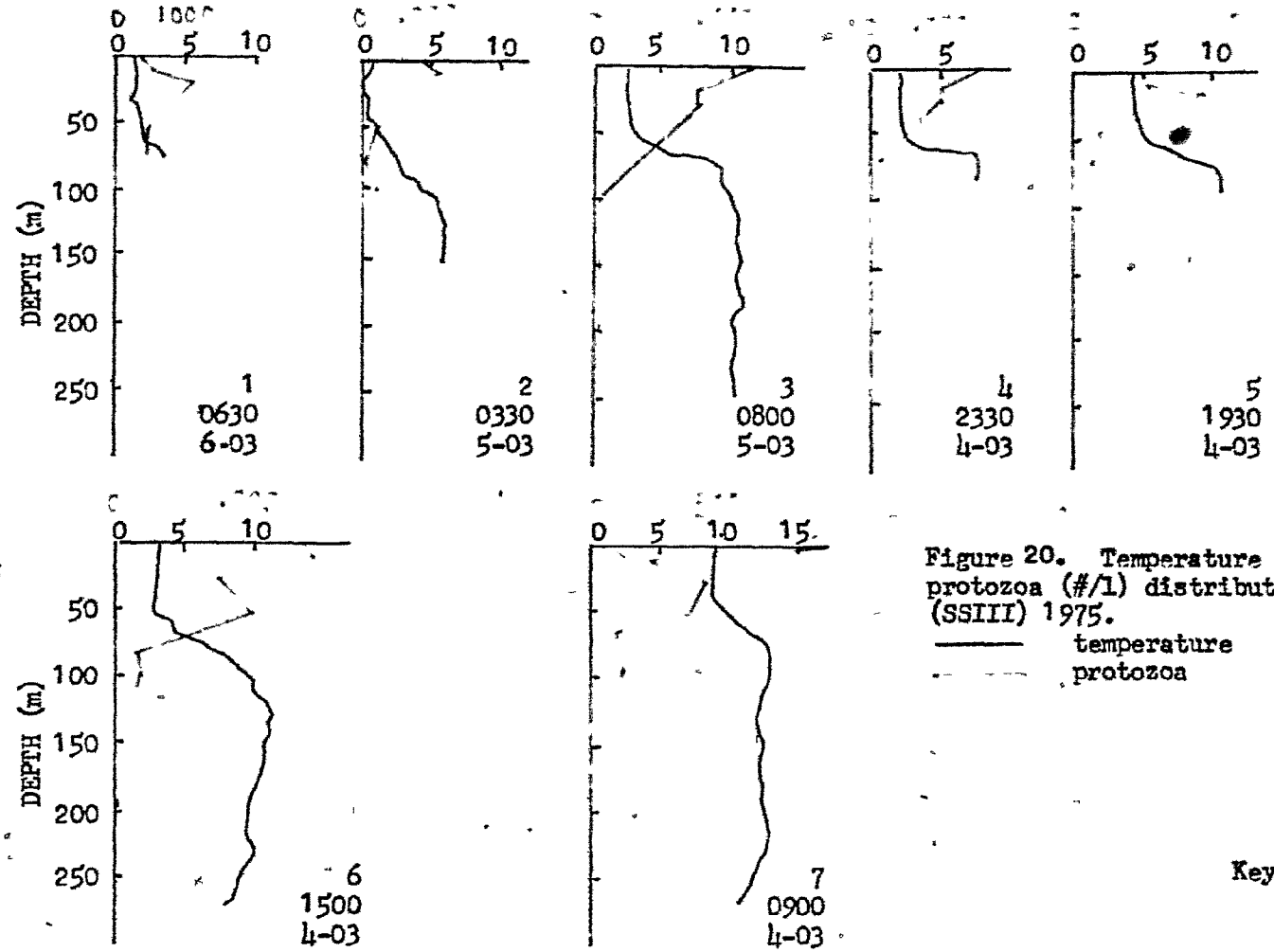


Figure 20. Temperature (C°) and protozoa (#/l) distribution: March (SSIII) 1975.

——— temperature

– – – – protozoa

Key: station #
time
day-month

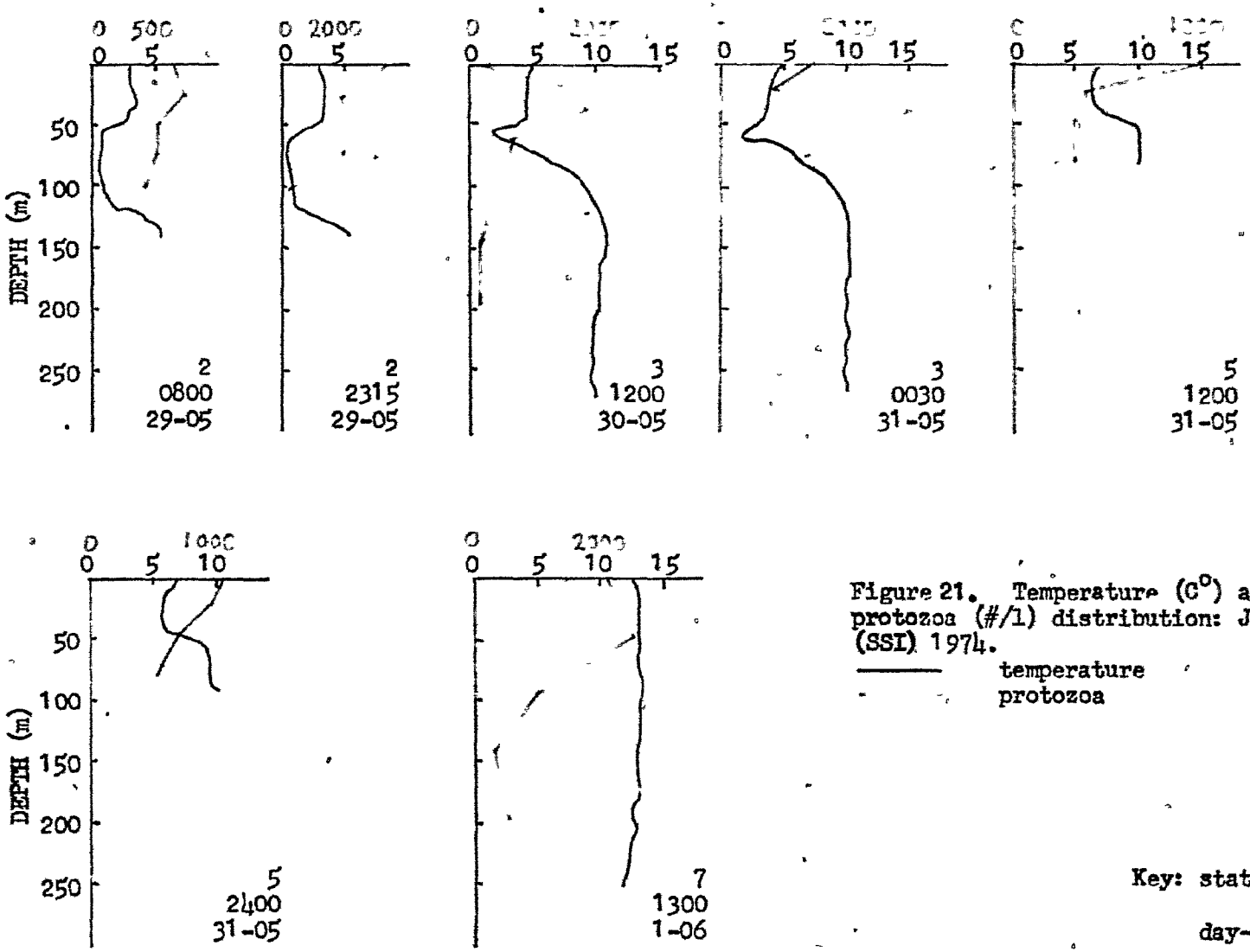


Figure 21. Temperature (C°) and protozoa (#/l) distribution: June (SSI) 1974.

——— temperature

- - - protozoa

Key: station #
time
day-month

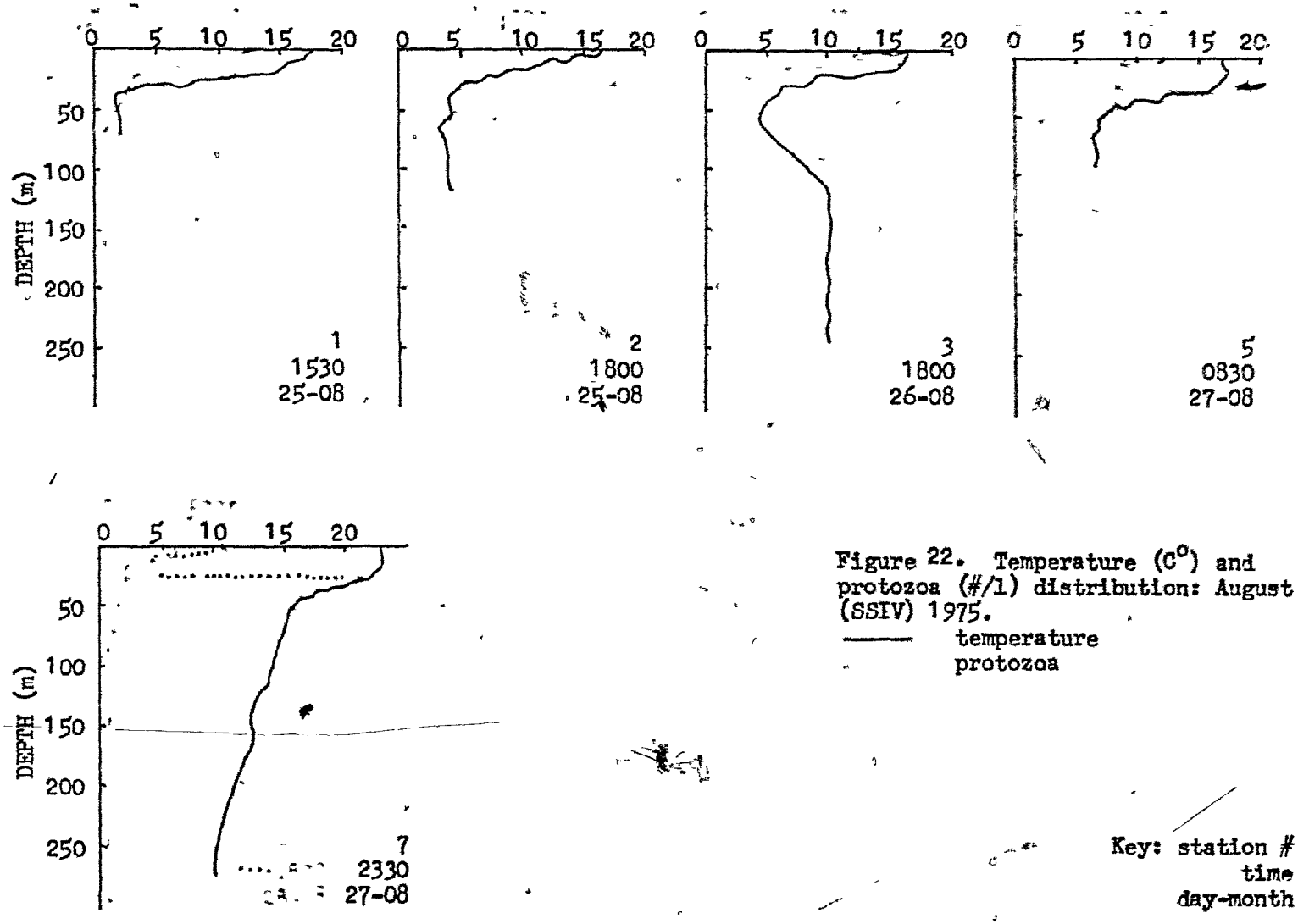


Figure 22. Temperature (C°) and protozoa (#/l) distribution: August (SSIV) 1975.

——— temperature

protozoa

Key: station #
time
day-month

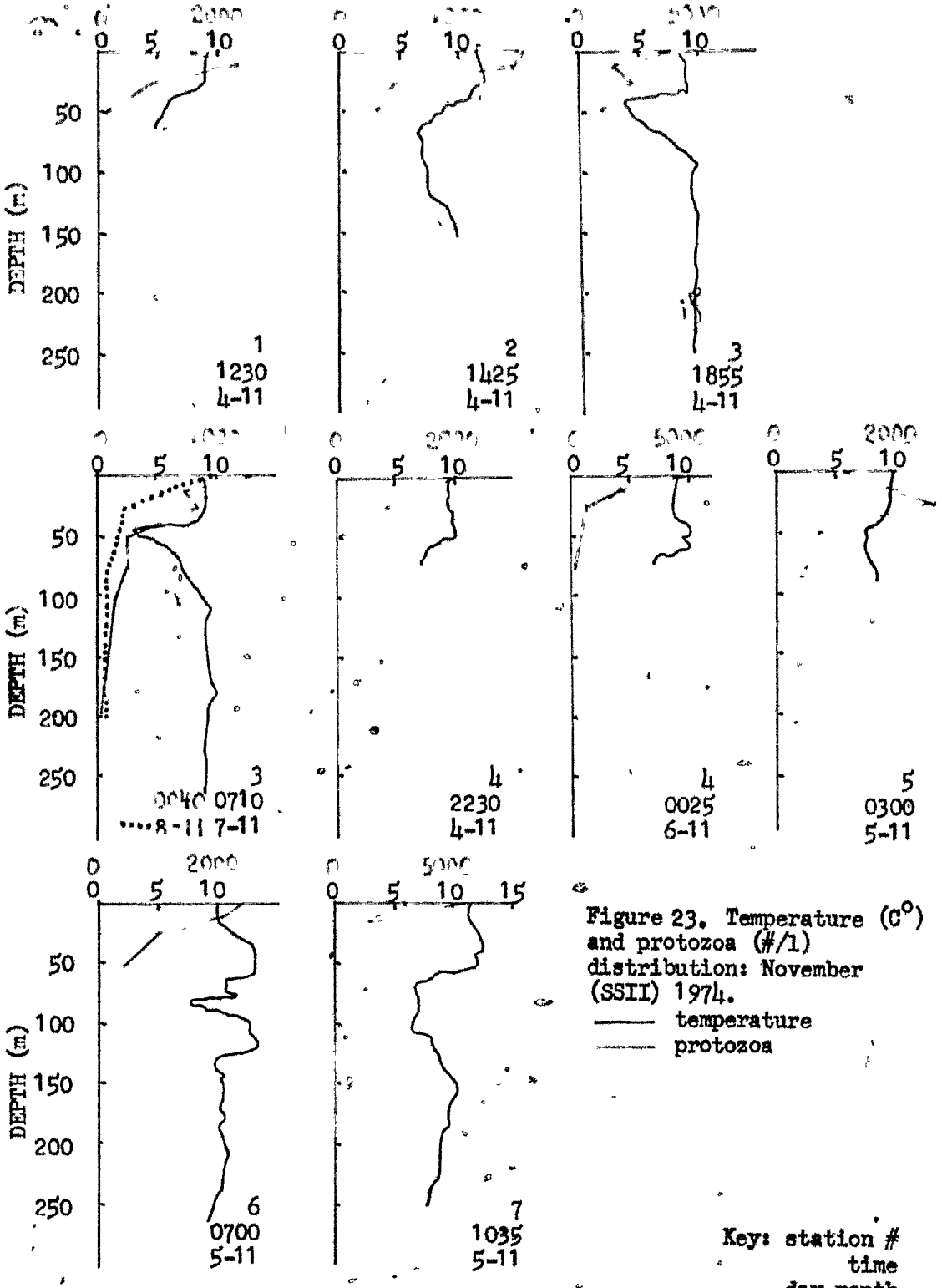


Figure 23. Temperature (C°) and protozoa (#/l) distribution: November (SSII) 1974.
—— temperature
—— protozoa

Key: station #
time
day-month

June. Only about half of the tintinnid species (one-third in March) were present at any one time. This situation parallels that found in the NWA. Generally there were more species to be found at the offshore stations (5-7) than at the inshore stations. Never more than about 25% (and usually less than 15%) of the total number of species were found at any one station.

The number of species per station was greatest during August when total protozoan abundance was highest. However, the species diversity as calculated using the Shannon-Wiener formula was highest during November. This was due to the dominance of a very few species (primarily the strombidia) during August. In November the abundance was more evenly distributed among the species and the number of species was relatively high. This situation parallels that found in the NWA where high abundance was often inversely correlated with diversity due to the dominance in the community of one or two protozoan species.

Generally, the greatest number of species as well as the highest diversity indices (and sometimes the greatest abundance) were to be found at the outermost stations (5-7). The increase in quantities offshore may be a result of favourable conditions produced by oceanic "fronts" (rather than typical coastal upwelling); i.e., the meeting of two different water types, thereby increasing nutrient supply and increasing primary production; or even perhaps advecting in an entire

protozoan community. The physical conditions in this area are not well understood and certainly deserve further study.

One of the more striking features of the data is the number of ephemeral species; i.e., species which are present only during a single cruise. These species are listed below along with the "omnipresent" species; i.e., those found during all four cruises.

SPECIES FOUND ONLY IN MARCH (SSIII)

Poroecus curtis (T)
Ptychocylis minor (T)
Tintinnopsis parvula (T)
Euplotes sexcostatus

SPECIES FOUND ONLY IN JUNE (SSI)

Candeina nitida
Ascampbella urceolata (T)
Dictyocysta speciosa (T)
Favella franciscana (T)
Parundella minor (T)
Proplectella parva (T)
Salpingella accuminata (T)
Salpingella curta (T)
Undellopsis pacifica (T)

SPECIES FOUND ONLY IN AUGUST (SSIV)

Xiphosphaera vesta (R)
Amphorella gaarderae (T)
Clymacocylis scalaroides (T)
Dadayiella bulbosa (T)
Dictyocysta reticulata (T)
Epiplocylis acuminata (T)
Eutintinnus fraknoi (T)
Parundella grandis (T)
Parundella subcaudata (T)
Proplectella globosa (T)
Proplectella subcaudata (T)
Salpingella gracilis (T)
Stenosemella ventricosa (T)
Stenostrupiella steenstrupi (T)
Tintinnopsis cylindrica (T)
Tricophrya columbiae

SPECIES FOUND ONLY IN NOVEMBER (SSII)

Coelancantha dogiella (R)
Coelodenorum furcatissima (R)
Phormacantha hystrix (R)
Lacrymaria olor
Strombidium cornucopiae
Codonella acuta (T)
Dictyocysta elegans (T)
Proplectella perpusilla (T)
Tintinnopsis pistilum (T)
Tintinnopsis strigosa (T)

SPECIES FOUND DURING ALL FOUR CRUISES

Lithoemlissa setosa (R)
Sticholonche zanclea (R)
Cyclotrichium meunieri
Tontonia gracillima
Acanthostomella norvegica (T)
Amphorella quadrilineata (T)
Protorhabdonella curta (T)
Strombidium sp.

Strombidium acuminata	Strombidium ovale
Strombidium calkinsi	Strombidium strobilus
Strombidium conicum	Strombidium sulcatum

T = tintinnid R = radiolarian

Almost half (39) of the total number of species can be classified as ephemeral whereas only 20% (14) are omnipresent. Of the latter group, half (7) are strombidia and only three are tintinnids. Although the sampling frequency is quite inadequate to draw any firm conclusions it should be pointed out that tintinnid species in the NWA appear and disappear very rapidly, some species being present only for a few days. Many radiolarians also exhibited this limited presence (most being present only in November).

The transience of species seems to be particularly well-marked for the tintinnid genus Dictyocysta. D. speciosa is found in June followed by D. reticulata in August followed by D. elegans in November. On the other hand, these species are somewhat similar and it is quite possible that they are merely phenotypes of the same species. Burkovsky (1973) has presented convincing arguments that eleven different species of Parafavella found in the White Sea at different times of the year are, in fact, phenotypes of P. denticulata. Proplectella species also seem to exhibit succession as follows: P. subacuta and P. tumida (March); P. parva and P. subacuta (June); P. globosa and P. subcaudata (August); P. perpusilla and P. tumida (November). Although two species are present at the same time, they tend to occupy different depths, as do the

co-occurring species of Acanthostomella, A. norvegica being found consistently in deeper water than A. conicoides.

The ephemeral species also tend to be somewhat restricted in their horizontal distribution while the omnipresent species also tend to be cosmopolitan. Many of the tintinnids are restricted to the outer stations except for those species belonging to the genus Tintinnopsis. Members of this genus with arenaceous or agglomerated loricae are in fact typically found inshore. Most of the NWA tintinnids belong to this group while the Scotian Shelf tintinnids exhibit a much greater proportion of species with hyaline or sculptured loricae. Gold and Morales (1976) have recently pointed out that such arenaceous and agglomerated forms are to be expected in shallow-water inshore areas where more of the particles which they cement onto their loricae are available.

It is interesting to note that Codonella acuta was only present in November when coccolithophorids comprised a large proportion of the phytoplankton. Species of Codonella are characterized by their tendency to cement coccoliths onto their loricae. On the other hand, it is somewhat puzzling as to why more of these coccolith-cementing species were not found at this time.

As in the NWA, the summer nanoplankton-protozoan dominance in the water column was evident on the Scotian Shelf during August. At this time there were very few macrozooplankton (Bohrer, personal communication), again paralleling the situation in the NWA. In March the phytoplankton was overwhelmingly

dominated by large chain-forming diatoms (Chaetoceros and Thalassiosira), with few nanoplankters evident--and few protozoa. This situation is also found in the NWA in early spring. This information emphasizes the importance of a suitable food source in controlling the abundance of microzooplankton.

Most of the species found in the NWA are also found on the Scotian Shelf, although in much smaller abundance on the Shelf. It is difficult to compare these results with those of earlier research efforts, due in part to changes in taxonomic policy and in part to differences in collecting methods.

Bigelow, Lillick and Sears (1940) found maximum numbers of protozoa in June-July and noted a three-week-long March peak of strombidia in the Gulf of Maine. Bigelow (1924), Gran (1933) and Gaarder (1946) reported the dominance of Parafavella, Ptychocylis and Acanthostomella among the tintinnids of the Gulf of Maine and the Newfoundland banks. My values for Acanthostomella abundance are rather higher than they reported but my values for the other two genera are much lower, perhaps a result of time of sampling.

Braarud (1935) reported a concentration of 2900 Helicostomella subulata/l outside the Bay of Fundy but this species is very rare on the Scotian Shelf (although it is the most abundant species in the NWA). Prakash (1963) reported large numbers of Favella in the Bay of Fundy during summer (enough Favella, in fact, to control Gonyaulax blooms), but this species was only found once (in June) on the Scotian Shelf and

never in the NWA, which may indicate a rather limited distribution of some genera. In general I found the same genera and often the same species of tintinnids and strombidia on the Scotian Shelf as have been reported by earlier workers investigating near-by areas.

SUMMARY

Although samples from only four cruises to the Scotian Shelf were examined it seems that the protozoan community there exhibits many of the trends evident in the investigations of NWA protozoa. Protozoa are most abundant during summer and fall when the phytoplankton is dominated by nanoplankton and macroplankton abundance is low. Many of the species (especially the tintinnids) are transient, appearing and disappearing very quickly. There is a large number of tintinnid species to be found but they are rarely very abundant whereas the strombidia are abundant, omnipresent and cosmopolitan. Abundance of protozoa is correlated with the type and abundance of food available to them, and their distribution may be modified by water mass boundaries.

4. TINTINNIDS AND OTHER PROTOZOA IN NAIN BAY, LABRADOR DURING OCTOBER, 1973.

INTRODUCTION

The future of Canadian oceanography is expected to concentrate more and more on the Arctic and other northern waters, yet these waters are relatively unexplored and little baseline information is available to judge the impact of civilization on, and increasing utilization of, these areas. As part of their training programme the Department of Oceanography at Dalhousie University organised a cruise to Nain Bay, Labrador aboard CSS Hudson during the period 15-30 October 1973.

Nain Bay is a Canadian fjord located at 56°30'N. It is 35.4 km in length, 1.6 km in width (average) with a limiting sill depth of 20 m. The main basin depth is 120 m. Nutt (1963) presented hydrographic data (i.e., temperature and salinity) for Nain Bay. He stated that the bay is covered with ice 5-7 months of the year and that the basin water is continuously renewed via turbulent mixing during winter and summer; hence it is never anoxic.

At the time, nothing was known of the chemical and biological characteristics of Nain Bay and the cruise was designed to investigate these parameters. The following is a description of the microzooplankton within Nain Bay and at a few oceanic stations taken on the way to the bay.

METHODS

Stations occupied on the way to Nain Bay included the following:

1. 43°57'N, 62°12'W (about 110 km east of Halifax), 15 Oct, 1630 hrs.
3. 48°21'N, 63°32'W (Cabot Strait), 17 Oct, 1500 hrs.
4. 52°30'N, 54°33'W (east of Belle Island), 18 Oct, 1300 hrs.
5. Off Port Williams, Nain Bay, 19 Oct, 1500 hrs.
6. 56°45'N, 59°05'W (shelf break, water depth: 182 m), 27 Oct, 1330 hrs.

N27. 56°31'N, 61°W (just outside the approaches to Nain, water depth: 91 m. This was the base line station for the Bay.), 26 Oct, 1200 hrs.

Figure 24 shows the locations of the stations within Nain Bay itself. The stations selected for observations of the protozoa were as follows:

N20.	24 October, 1330 hrs.
N19.	23 October, 1530 hrs. 51 m.
N10.	20 October, 1530 hrs. 70 m.
N7.	21 October, 1600 hrs. 38 m.

Sixty 500-ml samples were taken from the ten stations using 12-l Niskin bottles (and preserved with 1% Champy's fixative) from 0, 10, 20, 30, 50, 75 and 100 m. 400 ml were settled out and the protozoa were identified and enumerated at 200x using a Wild M-40 inverted microscope.

RESULTS

Forty-three species of protozoa were identified from the 10 stations, 40 of which were ciliates, 26 being tintinnids

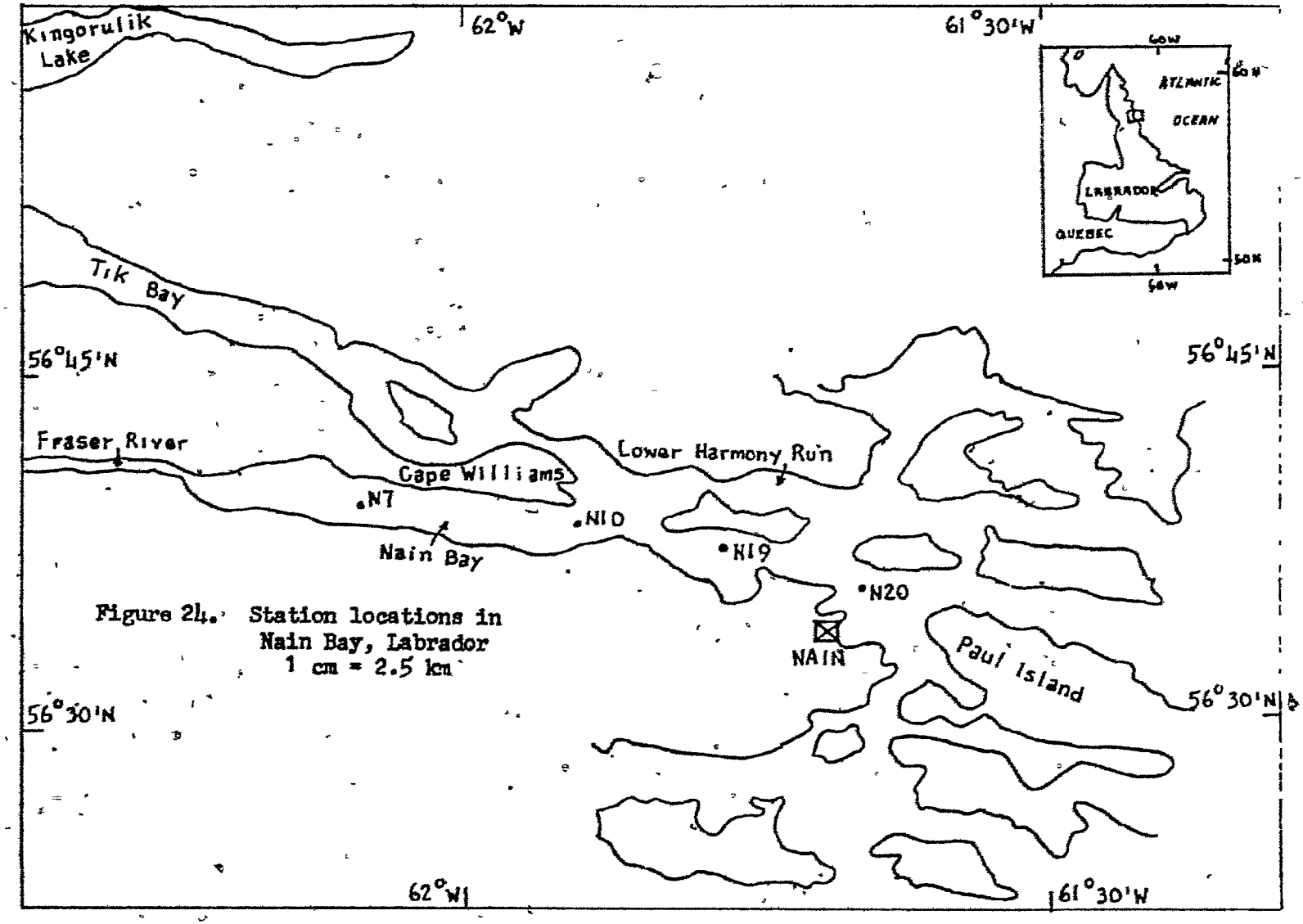


Figure 24. Station locations in Nain Bay, Labrador
1 cm = 2.5 km

and 8 being strombidia. Table 10 lists all the species identified as well as their maximum abundance at each station. Table 11 summarizes the enumerations and presents data on diversity for each station and depth sampled. Table 12 presents some general statistics of the cruise.

Tintinnids were quite scarce at this time of year, particularly in Nain Bay itself. Highest numbers of tintinnids were found at Station 3 (Cabot Strait) but even here their abundance did not exceed 600/l. Tintinnids were slightly more abundant at the northern oceanic stations in October than they were at the outer Scotian Shelf stations in November. Most of the tintinnid species tended to be oceanic, particularly Acanthostomella norvegica, Protorhabdonella curta, Ptychocylis drygalskii and Tintinnus tubulosus. Parafavella denticulata, Helicostomella and particularly Tintinnopsis, tended to be more common in the bay. Holmes (1956) listed Acanthostomella, Parafavella, Ptychocylis and Tintinnus as the most abundant tintinnid species at his Labrador Station B, located at 56°30'N, 51°W, at the same latitude but farther east than our Station N27.

The strombidia, though less abundant than in the North West Arm (NWA) at this time of year, were more abundant than on the Scotian Shelf in early November. As in other localities, the strombidia tended to be rather cosmopolitan but S. ovale, S. conicum, S. strobilus and particularly S. sulcatum were more abundant at the oceanic stations than inside

Table 10. Nain Bay Protozoa and their maximum abundance (#/l)

SPECIES	STATION NUMBER									
	1	3	4	5	6	N27	N20	N19	N10	N7
Phylum PROTOZOA										
Subphylum PLASMODROMA										
Class SARCODINA										
Subclass RHIZOPODA										
Order TESTACIDA										
Difflugia oblonga	18	18	18	107	36	36	90	54	143	90
Euglypha laevis		18								
Subclass ACTINOPODA										
Order RADIOLARIDA										
Sticholonche zanclea	36	179								
Subphylum CILIOPHORA										
Class CILIATA										
Subclass HOLOTRICHIDA										
Order GYMNOSTOMATIDA										
Cyclotrichium meunieri	18	609	609	215	233	376	2578	6534	6229	1128
Didinium nasutum		161					18	125		
Mesodinium pulex	179		36	18				18	54	54
Tiarina fusus				27					36	
Order HYMENOSTOMATIDA										
Frontonia marina		54	18	36			18	18		
Subclass SPIROTRICHA										
Order OLIGOTRICHIDA										
Strombidium sp.	644	841	555	519	734	591	1164	1235	1074	608
Strombidium acuminatum										18
Strombidium calkinsi	36	161	18		18		90	90	36	72
Strombidium conicum	18	877	179	322	197	251	304	125	107	72
Strombidium cornucopiae								18		
Strombidium ovale	591	841	322	358	125	36	179	179	125	18
Strombidium strobilus		143	340	18	54	54			54	18
Strombidium sulcatum	931	6444	895	3204	501	412	430	376	322	251
Tontonia gracillima	72	394	197	233	143	233	268	197	286	36
Order TINTINNIDA										
Acanthostomella norvegica	18	18	107	161	125	54				
Codonellopsis contracta		18								
Epiorella ralomensis			18							
Eutintinnus pacificus					18					
Helicostomella fusiformis							18			
Helicostomella subulata						18	18			
Metacylis corbula		54				18		18		
Parafavella denticulata						54	36		18	
Parafavella parumdentata		465	18	18			36			
Parundella lachmanni	18									
Parundella lata							18			
Proplectella parva	161				18					
Proplectella perpusilla								18		

Table 10. (continued)

SPECIES	STATION NUMBERS 1	3	4	5	6	N27	N20	N19	N10	N7
Proplectella tumida	18		18				36			36
Protorhabdonella curta	18	107								
Ptychocylis cylindrica					36	54	18			
Ptychocylis drygalskii		18	36	90	36	54	18			18
Salpingella acuminata					36					
Salpingella curta	18						18			
Tintinnopsis lata							18	18	36	18
Tintinnopsis parvula		18					36	18		
Tintinnopsis sacculus						18				
Tintinnopsis strigosa						18	18		18	36
Tintinnopsis wailesi									36	
Tintinnus tubulosus	18	18								
Undella columbiana			54		18	54				

Nain Bay, while Strombidium sp. was slightly more abundant in the bay. As in the NWA and on the Scotian Shelf strombidia characteristically comprised a substantial majority of the total protozoa at the oceanic stations. In the top 30 m of Station 5, for example, they comprised more than 90% of the total protozoa and the 80%+ values in the top 10 m of Station 3 were due almost entirely to the presence of S. sulcatum. Both Holmes (1956) and Bursa (1961) noted large abundances of S. conicum and other strombidia in the Labrador Sea and the waters around Igloolik respectively.

On the other hand, the prominence of the strombidia in Nain Bay was greatly reduced by the almost total dominance of the bay by Cyclotrichium meunieri, which exceeded 6000/l in the surface waters of two of the four stations. Bursa (1961) listed this species as the most common organism in the shallow

Table 11. General summary of the Nain Bay data

Z(m)	1	3	4	5	6	N27	N20	N19	N10	N7
				STATION NUMBER						
A.	Total number of protozoa per liter									
0	2481	4106	2685		1146	1038	3882	7842	2381	2025
10	2041	10919	2311	3974	2095	1774	3312	7876	6999	2024
20	788	3947	1522	3203	842	1541	3009	2812	2990	842
30			1253	1217	807	1164	2704	5434	3364	951
50	341	1754	1093	1369	771	842	4117	1611	3186	
75	180	1019	897	1253		752	4388		1809	
100	197	162		789	466		2078			
B.	Number of species observed									
0	9	14	11		8	8	14	11	6	8
10	9	14	10	4	12	11	12	10	10	10
20	8	14	9	5	8	11	7	9	9	8
30			8	5	7	8	10	10	11	12
50	5	12	10	9	8	8	12	5	11	
75	5	10	10	9		7	8		11	
100	5	3		10	3		10			
C.	Species diversity indices									
0	1.535	1.914	1.873		1.515	1.695	1.531	0.889	1.048	1.329
10	1.661	1.534	1.935	0.693	1.905	1.896	1.363	0.726	0.537	1.424
20	1.561	1.744	1.758	0.632	1.663	1.747	1.284	1.189	1.247	1.560
30			1.561	1.141	1.361	1.505	1.371	0.986	1.310	1.467
50	1.239	1.996	1.512	2.028	1.592	1.677	1.300	1.028	1.160	
75	1.359	1.971	1.528	1.924		1.616	1.108		1.541	
100	1.298	0.977		2.265	0.899		1.423			
D.	Number of tintinnids per liter									
0	143	286	90		18	72	108	0	0	0
10	197	573	108	0	179	162	72	0	0	36
20	90	233	125	0	36	108	18	18	18	36
30			54	0	18	90	36	9	18	108
50	0	36	72	161	36	108	36	0	18	
75	18	54	126	179		72	54		72	
100	18	18		233	36		54			
E.	Number of strombidia per liter									
0	2032	3285	1843		1002	715	1575	1451	1182	753
10	1611	9200	1558	3759	1504	1200	1342	1145	483	914
20	680	2541	967	3096	716	1039	1111	824	668	555
30			895	1110	627	626	1271	1442	984	734
50	287	966	877	698	681	412	1414	769	1056	
75	108	447	645	716		376	1684		787	
100	161	54		412	430		967			
F.	Percent of total protozoa comprised of *Cyclotrichium meunieri*									
0	0	7	23		8	9	52	78	45	56
10	1	6	24	5	11	18	56	83	69	49
20	0	10	25	3	4	21	54	67	63	15
30			9	9	4	33	48	71	61	2

Table 11. (continued)

Z(m)	1	3	4	5	6	N27	N20	N19	N10	N7
50	0	8	7	14	2	19	57	50	60	
75	0	26	10	9		10	59		44	
100	0	0		2						
G.	Percent of total protozoa comprised of tintinnids									
0	6	7	3		2	7	3	0	0	0
10	10	5	5	0	9	9	2	0	0	2
20	11	6	8	0	4	7	1	1	1	4
30			4	0	2	8	1	0	1	11
50	0	2	7	12	5	13	1	0	1	
75	10	5	14	14		10	1		4	
100	9	11		30	8		3			
H.	Percent of total protozoa comprised of strombidia									
0	82	80	69		87	69	41	19	50	37
10	79	84	67	95	72	68	41	16	7	45
20	86	64	64	97	85	67	37	29	22	66
30			71	91	78	54	47	27	29	77
50	84	55	80	51	88	49	34	48	33	
75	60	44	72	57		50	38		44	
100	82	33		52	92		47			

(<50 m) waters around Igloolik. Cyclotrichium is usually not very abundant on the Scotian Shelf but as in Nain Bay it tended to dominate the protozoan community of the NWA (in even greater numbers) at this time of the year. Cyclotrichium is also not very common at the northern oceanic stations.

DISCUSSION

The reasons for the absence of the tintinnids in Nain Bay proper may be gleaned from a consideration of other data kindly supplied to me by Dr. Robert O. Fournier. Temperature data reveal that the bay was almost isothermal at about 3.5° C during late October, and was thus well-mixed. The 1% light level was at about 30 m throughout the bay. Nitrate values were usually 0.75 µM/l or more; ammonia concentrations generally

Table 12. General statistics concerning the Nain Bay data.

	#	STATION #	DEPTH (m)
Number of samples	60		
Number of protozoan species	43		
Number of tintinnid species	26		
Maximum number of protozoa/l	10919	3	10
Minimum number of protozoa/l	162	3	100
Maximum number of species/station	14	3	0,10,20
		N20	0
Minimum number of species/station	3	6	100
Maximum species diversity index	2.265	5	100
Minimum species diversity index	0.537	N10	10
Maximum number of Cyclotrichium/l	6534	N19	10
Minimum number of Cyclotrichium/l	0	1	0,20,50, 75,100
		6	100
Maximum number of tintinnids/l	573	3	10
Minimum number of tintinnids/l	0	1	50
		5	10,20,30
		N19	0,10,50
		N10	0,10
		N7	0
Maximum number of strombidia/l	9200	3	10
Minimum number of strombidia/l	54	3	100
Maximum per cent Cyclotrichium	89	N10	10
Minimum per cent Cyclotrichium	0		
Maximum per cent tintinnids	30	5	100
Minimum per cent tintinnids	0		
Maximum per cent strombidia	97	5	20
Minimum per cent strombidia	7	N10	10

exceeded 1 µM/l; the phytoplankton was dominated by diatoms ranging in concentration from 19,000/l at Station N7 to 95,000/l at Station N10; hence we may have arrived in Nain toward the decline of the fall bloom. Dinoflagellate concentrations were usually less than 1000/l. However, most important was the fact that flagellates (nanoplankters) were very low in numbers; i.e., less than 4000/l. As on the Scotian Shelf and in the NWA there is an indication here that tintinnid abundance is

influenced in part by presence of a suitable food source.

The reasons for the dominance of Cyclotrichium in Nain Bay are not at all clear. As was pointed out in a previous section, nothing is known of the nutrition of these organisms and food vacuoles have not been observed inside them. Perhaps their occasional abundance in bays such as Nain, the NWA and Wellington Harbour (Bary and Stuckey 1950) is related to a need for a rather organically-rich environment. MacKinnon (personal communication) reports total organic carbon values of 1.2-1.5 ppm in the surface waters of Nain Bay, values comparable to those found in the NWA.

Species diversity, as calculated using the Shannon-Weiner formula, was greater at the oceanic stations than at the Nain Bay stations, due entirely to the dominance of the bay protozoa by the single species of Cyclotrichium. Lowest diversity of the oceanic stations was at Station 5 as a result of the large numbers of Strombidium sulcatum there. The diversities at the oceanic stations were comparable to those on the Scotian Shelf in November while the diversities at the Nain Bay stations were comparable to those found in the NWA during late October, when Cyclotrichium also may dominate the latter and decrease diversity. As in other areas, samples which included the largest numbers of individuals more often than not exhibited the lowest species diversity indices, a phenomenon noted by Holmes (1956) among the Labrador Sea protozoa.

Little can be said of the protozoan community as a functional unit of the food web in northern waters or in Nain Bay

based on the data of a single cruise at a single point in time. However, what can be said is that this cruise offered no surprises, no vast deviations from what might have been expected, given the knowledge of which tintinnid species tend to be found at northern latitudes; given the knowledge of the state of affairs at this time of year in the NWA and on the Scotian Shelf; given the vagaries of the distribution of strombidia and Cyclotrichium; and given the minimum generalities of the phytoplankton complement to be found in the Bay.

5. TINTINNID FEEDING

INTRODUCTION

Utermohl analysis of water bottle collected samples from the North West Arm of Halifax Harbour has produced the following observations:

1) Tintinnids are most abundant from June until October (Fig. 3).

2) Net phytoplankton are rather scarce during summer (especially during July and August).

3) The summer phytoplankton is dominated by nanoplankters (Fig. 3). and nanoplankton blooms are quickly followed by tintinnid bursts of growth.

4) Adult copepods are most abundant from June until October (Appendix A, Fig. 27) with copepod peaks more or less corresponding to tintinnid peaks but occasionally being slightly later.

The form of the seasonal cycles suggests that nanoplankton constituted the basic food supply of both ciliates and copepods and that their feeding activities were responsible for the termination of the nanoplankton blooms. This is analogous to spring zooplankton peaks, which commonly follow the spring diatom flowering and are believed in some cases to terminate it by their grazing activities.

Whether the copepods were also obtaining a significant amount of food from tintinnids is problematical. The absolute

coincidence of July peaks shows that copepod feeding activity was not able to prevent a major burst of tintinnid growth. The slight lags that can be observed in the March and September peaks might indicate significant predation or might simply be the result of a slower growth cycle in copepods.

The problem of copepods feeding on tintinnids has not been studied in the laboratory because of difficulties in maintaining stable cultures for feeding experiments and because analyses of gut contents of preserved animals are unsatisfactory. Loricate tintinnids are too large to be ingested whole, and loricae are probably crushed, with subsequent ingestion of only the soft body.

Despite the fact that the inter-relations between these two animal populations are not well understood, the great abundance of ciliates in the North West Arm suggests the possibility that they are the most important factors in controlling nanoplankton populations and can do so with such rapidity as to produce mass starvation and a decline in their own populations. Thus the quantitative significance of tintinnid feeding will be discussed further in the present section.

Observations of individual tintinnids fully packed with food organisms (Appendix B, Figs. 18 and 19) and the rather high rates of excretion by tintinnids seem to indicate that they have a relatively high food requirement. Both Zeitzschel (1967) and Gold (1968) have stressed the need for information about the feeding biology of tintinnids.

There are few papers dealing with feeding by ciliates. Pavlovskaya (1963) has discussed feeding of some Black Sea littoral ciliates and Fenchel (1968) has worked with some benthic ciliates. Hamilton and Preslan (1969) presented data for the marine ciliates Uronema. However, most of these ciliates are bacteria-feeders. Goulder (1962, 1973) has estimated feeding rates of Loxodes, a fresh-water pelagic ciliate and Rapport, Berger and Reid (1972) presented feeding data on Stentor.

Only two papers deal with feeding by tintinnids--Spittler (1973) and Blackbourn (1974). Spittler pointed out that tintinnids are selective feeders (i.e., they consume individual particles, may actively seek out a single food item and may reject an encountered unsuitable particle) rather than suspension feeders and that tintinnids probably do not preferentially consume bacteria or detritus but primarily seek out algal cells of 2-20 μ size. He determined ingestion rates for several tintinnid species and found that feeding is discontinuous at high food concentrations ($>10^5$ cells/ml).

Blackbourn's work was much more extensive and quantitative. He determined feeding rates primarily of Tintinnopsis subacuta and found that tintinnids could select one type of food in preference to another. Unlike Spittler, Blackbourn found no minimum size of food for tintinnids and concluded that all species consumed bacteria and detritus. He also found that temperature did not affect ingestion rates but

that digestion occurred more rapidly at high temperatures. He finally concluded that natural populations of tintinnids could decimate natural populations of nanoplankton in less than 24 hours in British Columbian waters.

While I was engaged in these feeding experiments, I did not have access to Blackbourn's thesis and I was uncertain of the meaning of Spittler's results because he used yeast as a food source. I thought it might be more realistic to use phytoplankton so that my experiments are more comparable to those of Blackbourn, although my methods were indirect rather than direct.

METHODS

Tintinnids were isolated from plankton tows using drawn-out pipettes under a dissecting microscope. They were placed in 8 ml of filtered sea water in 125-ml screw top test tubes. 2 ml of the food suspension were added and the tubes were placed in the dark in a 10° C incubator. The animals were allowed to feed for 6-9 hours. Controls consisted of 8 ml of filtered sea water and 2 ml of the food suspension. Food concentrations in the tubes before and after feeding were determined using a hemacytometer.

$$\text{Feeding rate/tintinnid} = \frac{\frac{C_2 E_1}{C_1} - E_2}{tT}$$

where: C_1, C_2 = food concentration in initial and final controls (#/ml),

E_1, E_2 = food concentration in initial and final experiments

t = time (hrs)

T = number of tintinnids/ml

This equation (Blackbourn 1974) carries the following assumptions: (a) the food concentration is above the optimum food concentration; (b) the food concentration is not inhibitory; and (c) the tintinnids feed at a constant, optimum rate.

RESULTS

The results of the feeding experiments are presented in Tables 13 and 14. Most of the data concern Helicostomella subulata, the most abundant tintinnid species found in the North West Arm. This species consumed 0-75% of its body volume in algal cells per hour with filtering rates of 0-5 µl/hr/tintinnid. Figure 25 is a histogram of the percentage of tintinnid volume consumed per hour for all species. Helicostomella can consume up to 50 Dunaliella, 170 Isochrysis, 11 Monochrysis, 46 Platymonas, or 3 Rhodomonas cells/hr.

DISCUSSION

The results are both extremely variable and extremely high in some cases. Table 15 presents data from other sources. Goulder's feeding rates were calculated from loss rates and are almost certainly too low. Blackbourn's data were also very variable (even more than mine in some cases but this is probably due to his more extensive investigations). For example, the range of feeding rates for Tintinnopsis subacuta

Table 13. Results of tintinnid feeding experiments

DATE (1975)	INITIAL FOOD CONC. $x10^4$/ml	TINTINNID SPECIES (AND #) INVOLVED	FEED. TIME (HRS)	TINTINNID VOLUME PER ML (μ^3)	VOLUME OF FOOD CONSUMED (μ^3/ml/hr)	% TINTINNID VOLUME CONSUMED PER HR
1. FOOD ORGANISM: DUNALIELLA (cell volume: 200 μ^3)						
25 Aug	1.71	Hs(164)Pg(1)	6	375,360	13,200	3.5
25 Aug	1.77	Hs(184)	6	372,641	128,780	34.6
1 Sept	1.09	Hs(185)Pg(74)	6	3,573,193	181,320	5.1
1 Sept	1.20	Hs(295)Pg(5)	6	913,557	194,640	21.3
1 Sept	1.53	Hs(246)	6	499,571	135,020	27.0
3 Sept	1.36	Pg(129)Hs(54)	9	5,685,472	59,360	1.0
4 Sept	1.41	Hs(199)Pg(59)	9	2,953,195	16,620	0.6
10 Sept	0.77	Hs(235)	7	475,927	0	0
10 Sept	0.73	Hs(231)Tp(1)Pg(1)	7	513,728	23,820	4.6
10 Sept	0.64	Hs(200)	7	405,044	143,540	35.4
18 Sept	1.20	Hs(249)Tp(1)	9	506,958	44,440	8.8
18 Sept	1.13	Hs(182)	9	368,590	91,800	24.9
4 Oct	1.95	Tp(112)Hs(106)	9	515,211	152,100	29.5
4 Oct	2.18	Hs(62)Tp(41)	9	235,366	131,340	55.8
12 Oct	2.59	Hs(216)Tp(16)	7	481,498	49,500	10.3
12 Oct	2.89	Hs(149)Tp(9)	7	326,698	168,920	51.7
2. FOOD ORGANISM: ISOCHRYSIS GALBANA (cell volume: 50 μ^3)						
21 July	6.18	Tp(64)Hs(56)	6	279,944	41,390	14.8
4 Aug	4.49	Hs(78)Tp(33)	9	246,345	34,155	13.9
4 Aug	7.31	Hs(139)Tp(6)	9	298,347	139,270	46.7
12 Oct	10.78	Hs(149)Tp(9)	7	326,689	44,075	13.5
12 Oct	8.54	Hs(216)Tp(16)	7	481,498	88,040	18.3
3. FOOD ORGANISM: MONOCHRYSIS LUTHERI (cell volume: 50 μ^3)						
18 Aug	3.79	Hs(107)Tp(2)	6	222,055	0	0
18 Aug	4.32	Hs(104)	6	210,623	0	0
18 Aug	4.16	Hs(128)	6	259,228	8,035	3.1
30 Sept	1.45	Hs(300)Tp(5)Ts(3)	14	629,651	0	0
30 Sept	1.74	Hs(270)Ts(3)Tp(1)	14	558,181	8,830	1.6
4. FOOD ORGANISM: PLATYMONAS TETRAHELE (cell volume: 300 μ^3)						
13 July	1.93	Hs(101)Tp(22)	6	264,027	0	0
28 July	2.33	Hs(112)Tp(92)	6	473,833	180,090	38.0
28 July	2.42	Hs(112)Tp(50)Tv(1)	6	362,361	274,920	75.9
4 Oct	2.34	Hs(293)Tp(9)	9	619,121	261,780	47.1
5. FOOD ORGANISM: RHODOMONAS LENS (cell volume: 300 μ^3)						
21 July	0.43	Tp(75)Hs(54)	6	296,926	0	0
28 July	1.02	Tp(112)Hs(45)	6	391,333	16,230	4.1
12 Sept	0.80	Hs(226)Tp(3)Ts(1)	22	468,632	4,590	1.0
6. FOOD ORGANISM: RHODOMONAS LENS AND PLATYMONAS TETRAGELE						
11 Oct	4.70	Tp(149)Hs(43)	9	486,123	176,400	36.3
11 Oct	5.14	Tp(156)Hs(24)	9	466,524	237,900	51.0
11 Oct	4.79	Tp(141)Hs(101)	9	582,161	353,220	60.7

Table 13. (continued)

DATE (1975)	INITIAL FOOD CONC. $X10^4$/ml	TINTINNID SPECIES (AND #) INVOLVED	FEED. TIME (HRS)	TINTINNID VOLUME PER ML (μ^3)	VOLUME OF FOOD CONSUMED (μ^3/ml/hr)	% TINTINNID VOLUME CONSUMED PER HR
7. FOOD ORGANISM: PYRAMIMONAS (cell volume: 140 μ^3)						
4 Aug	1.64	Hs(202)Tp(3)	9	417,129	56,448	13.5
8. FOOD ORGANISM: RHODOSORUS (cell volume: 140 μ^3)						
21 July	1.13	Tp(89)	6	403,022	63,938	15.9

Hs = Helicostomella subulata (animal volume: 18,279 μ^3)

Pg = Parafavella gigantea (animal volume: 389,010 μ^3)

Tp = Tintinnopsis parvula (animal volume: 24,103 μ^3)

Ts = Tintinnopsis strigosa (animal volume: 26,080 μ^3)

Tv = Tintinnopsis vasculum (animal volume: 9,072 μ^3)

was 3.3-38 µl/hr/tintinnid and maximum consumption obtained was 9.29% of T. subacuta body volume (10.13% of T. parvula body volume) per hour. Spittler made no mention of variability in his results. Assuming a volume of 65 μ^3 for an average yeast cell, a volume of 98,800 μ^3 for an average Tintinnopsis tubulosa (without its lorica), and a maximum feeding rate of 60 yeasts/hr/tintinnid, then T. Tubulosa can consume 5.26% of its body volume/hr. Spittler also reported a maximum filtering rate of 0.5 µl/hr/Leprotintinnus bottnicus, 0.8 µl/hr/T. tubulosa, 1.7 µl/hr/T. parvula and 8.5 µl/hr/T. fimbriata. He also found a decline in filtering rate at food concentrations of 10^3-10^4 cells/ml but concluded that tintinnids were not damaged after feeding for 24 hours at food concentrations

Table 14. Feeding rates of tintinnids

TINTINNID	# OF TINTINNIDS PER ML	FOOD	# OF FOOD/ ML ($\times 10^4$)	FEED. TIME (HRS)	FEEDING RATE (#/ HR/ TINTINNID)	FEEDING RATE (ML/ HR/ TINTINNID)
Hs	20.57	Dun	1.71	6	3.2	0.00019
Hs	20.44	Dun	1.77	6	31.5	0.00178
Hs	44.61	Dun	1.20	6	21.8	0.00182
Hs	27.33	Dun	1.53	6	24.7	0.00161
Hs	26.11	Dun	0.77	7	0	0
Hs	28.18	Dun	0.73	7	4.2	0.00058
Hs	22.22	Dun	0.64	7	32.3	0.00505
Hs	27.81	Dun	1.20	9	8.0	0.00067
Hs	20.22	Dun	1.13	9	22.7	0.00201
Hs	27.96	Dun	1.95	9	27.2	0.00139
Hs	12.81	Dun	2.18	9	51.2	0.00235
Hs	26.31	Dun	2.59	7	9.4	0.00036
Hs	17.41	Dun	2.89	7	48.5	0.00168
Pg	14.62	Dun	1.36	9	20.3	0.00149
Pg	7.59	Dun	1.41	9	10.9	0.00077
Tp	21.50	Dun	1.95	9	35.4	0.00182
Tp	9.86	Dun	2.18	9	66.6	0.00306
Hs	15.47	Iso	6.18	6	53.5	0.00087
Hs	13.43	Iso	4.49	9	50.7	0.00113
Hs	16.31	Iso	7.31	9	170.8	0.00234
Hs	17.41	Iso	10.78	7	50.6	0.00047
Hs	26.31	Iso	8.54	7	66.9	0.00078
Tp	11.90	Iso	6.18	6	69.6	0.00113
Tp	10.33	Iso	4.49	9	66.1	0.00147
Hs	12.18	Mono	3.79	6	0	0
Hs	11.56	Mono	4.32	6	0	0
Hs	14.22	Mono	4.16	6	11.3	0.00027
Hs	34.52	Mono	1.45	14	0	0
Hs	30.61	Mono	1.74	14	5.8	0.00033
Hs	14.40	Platy	1.93	6	0	0
Hs	25.75	Platy	2.33	6	31.1	0.00133
Hs	19.72	Platy	2.42	6	46.5	0.00192
Hs	33.86	Platy	2.34	9	25.8	0.00110
Tp	19.80	Platy	2.33	6	40.4	0.00173
Tp	15.13	Platy	2.42	6	66.6	0.00250
Hs	16.83	Rhod	0.43	6	0	0
Hs	21.18	Rhod	1.02	6	2.6	0.00025
Hs	25.70	Rhod	0.80	22	0.6	0.00008
Tp	12.95	Rhod	0.43	6	0	0
Tp	16.29	Rhod	1.02	6	3.3	0.00032
Tp	20.23	Platy,Rhod	4.70	9	29.1	0.00062
Tp	19.38	Platy,Rhod	5.14	9	40.9	0.00080
Tp	24.30	Platy,Rhod	4.79	9	48.5	0.00101

Table 14. (continued)

TINTINNID	# OF TINTINNIDS PER ML	FOOD	# OF FOOD/ ML ($\times 10^4$)	FEED. TIME (HRS)	FEEDING RATE (#/ HR/ TINTINNID)	FEEDING RATE (ML/ HR/ TINTINNID)
Hs	26.30	Platy,Rhod	4.70	9	22.4	0.00048
Hs	25.20	Platy,Rhod	5.14	9	31.5	0.00061
Hs	31.59	Platy,Rhod	4.79	9	37.3	0.00078
Hs	22.88	Pyr	1.64	9	17.6	0.00107
Hs	22.08	Rhodos	1.13	6	20.1	0.00178
Tp	16.98	Rhodos	1.13	6	26.9	0.00238

Hs = Helicostomella subulata
Pg = Parafavella gigantea
Tp = Tintinnopsis parvula

Dun = Dunaliella
Iso = Isochrysis galbana
Mono = Monochrysis lutheri
Platy = Platymonas tetrahele
Rhod = Rhodomonas lens
Pyr = Pyramimonas
Rhodos = Rhodosorus

of 10^6 cells/ml. Furthermore, Spittler determined that ingestion rates of T. tubulosa were constant at food concentrations up to 3.74×10^4 cells/ml but that this species stopped feeding after about 90 minutes at food concentrations of 3.75×10^5 cells/ml having consumed about 95 cells/tintinnid during this time. Neither my data nor Blackbourn's data show any consistent relationship between feeding rate and initial food concentration although Blackbourn felt that Monochrysis concentrations of 2.1×10^5 cells/ml were inhibitory to Helicostomella kiliensis. The closest I came to this was 1.78×10^5 Isochrysis/ml and this was certainly not inhibitory to H. subulata.

Blackbourn estimated that T. subacuta would reach a steady state feeding rate after feeding for about 3 hours and that the optimum food concentration was always $<10^4$ cells/ml. All

Figure 25.

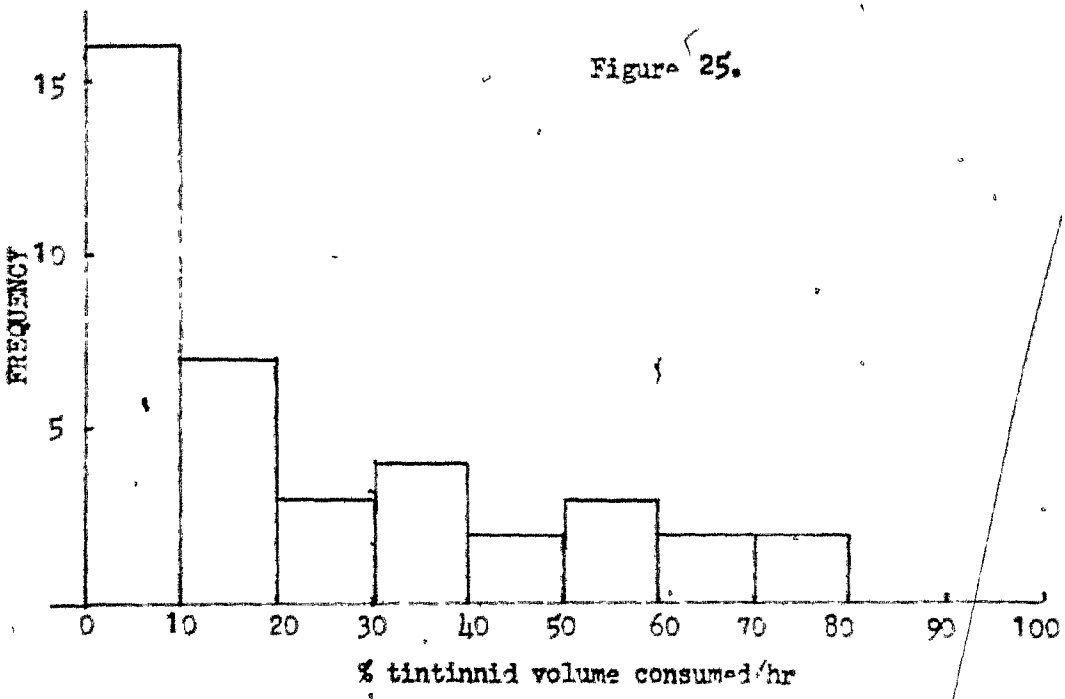


Figure 26. Tintinnopsis parvula

Figure 27. Tintinnopsis sacculus

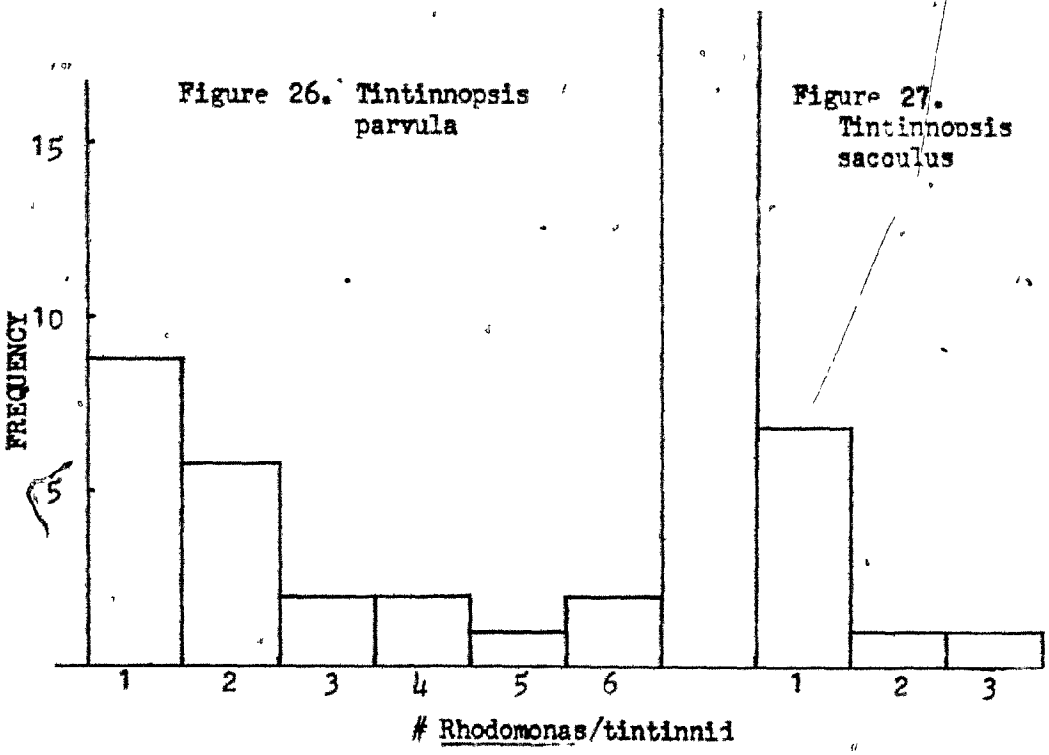


Table 15. Previous results of protozoan feeding rates

PREDATOR	PREY	INITIAL FOOD CONC. $x10^4$/ml	FEEDING RATE (# /HR/ ANIMAL)	VOLUME OF FOOD CONSUMED (μ^3/HR/ ANIMAL)	% ANIMAL VOLUME CONSUMED PER HR	FEEDING RATE (ML/HR/ ANIMAL)	SOURCE
Ts	Dt	0.17	32.5	6,500	9.29	0.0065	Blackburn (1974)
Ts	Dt	1.56	25.1	5,020	7.17	0.0018	"
Ts	Dt	0.44	9.7	1,940	2.77	0.00034	"
Ts	Dt	0.62	2.0	400	0.57	0.0003	"
Ts	Ig	6.60	26.3	1,315	1.88	0.00004	"
Ts	Ig	6.60	46.7	2,335	3.34	0.00011	"
Ts	Ml	0.80	26.0	1,300	1.86	0.0018	"
Ts	Ml	1.30	26.5	1,325	1.89	0.002	"
Ts	Ml	0.5	17.4	875	1.25	0.0017	"
Ts	Ml	1.60	24.2	1,210	1.73	0.0010	"
Tp	Dt	0.39	1.5	300	1.00	0.0004	"
Tp	Dt	0.78	2.4	480	1.60	0.0003	"
Tp	Ml	7.35	5.7	285	0.95	0.0002	"
Tp	Ml	0.70	60.8	3,040	10.13	0.0082	"
Hk	Ml	4.10	1.7	85	0.21	0.00004	"
Hk	Ml	10.90	0	0	0	0	"
Hk	Ml	21.30	0.8	0	0	0	"
Hk	Ml	0.50	6.7	335	0.81	0.0013	"
Tr	Dt	0.62	0	0	0	0	"
Tr	Ml	1.30	6.5	325	5.42	0.0005	"
Sc	Te		32	988,864	1.51		Papport (1972)
Sc	Eg		41	149,035	0.23		"
Sc	Cp		59	220,601	0.34		"
Sc	Cr		328	97,744	0.15		"
Lm	Sd			1,429	0.01		Goulder (1972)

Species	Volume (u^3)
Ts = Tintinnopsis subacuta	70,000
Tp = Tintinnopsis parvula	30,000
Hk = Helicostomella kiliensis	40,000
Tr = Tintinnopsis rapa	6,000
Sc = Stentor coeruleus	65,416,667
Lm = Loxodes magnus	24,531,250
Dt = Dunaliella tertiolecta	200
Ig = Isochrysis galbana	50
Ml = Monochrysis lutheri	50
Te = Tetrahymena pyriformis	30,902
Eg = Euglena gracilis	3,635
Cp = Chilomonas paramecium	3,749
Cr = Chlamydomonas reinhardti	238
Sd = Scenedesmus denticulatus	4,764

of my experiments lasted much longer than 3 hours and food concentrations were almost always above this optimum level. Thus, my values may represent the maximum rates possible.

There are many factors which might affect apparent feeding rates of tintinnids, including the method used to determine the rate. Spittler allowed his animals to feed for 3 minutes to 4 hours, then killed them and counted the number of Congo red-stained yeast cells inside the animals. Blackbourn watched a single tintinnid for a time and counted the number of food organisms it appeared to ingest, or else he allowed them to feed for a time and then counted the number of food organisms inside. These are all direct measurements and might be expected to be more reliable than the more indirect methods I used. However, Blackbourn admitted that his methods were rather subjective and that he could have missed the ingestion of some very small particles.

It is difficult to determine the effects of mechanical manipulation of the tintinnids. Short term experiments may not allow sufficient time for the animals to recover from mechanical shock, if in fact it occurs. If the tintinnid does not feed at all or feeds very slowly until it recovers, short term experiments could vastly underestimate the normal feeding rate. Longer experiments give the animals time to recover and perhaps feed at a more normal rate. Microscopic examination of the tintinnids after 9 hours showed that they were in very good condition, often packed with food cells, and swimming normally.

Another factor to consider is that these experiments really dealt with rather small entities so that quantities must be expressed as precisely as possible. For example, it is not possible to compare food volume consumed with lorica volume because the animal rarely fills a constant proportion of the lorica. Thus, only the soft body should be considered, a difficult thing to determine if the lorica is of the arenaceous type. Blackbourn reported the volumes of Tintinnopsis parvula and Helicostomella kiliensis to be $3x10^4$ and $7x10^4$ μ^3, respectively. I have determined North West Arm T. parvula volume to be $2.41x10^4$ μ^3 (based on measurements of 40 animals, assuming a cylindrical body) and H. subulata (probably the same species as H. Kiliensis) volume to be $1.83x10^4$ μ^3 (based on measurements of 48 animals). Were I to use Blackbourn's "order of magnitude" estimates, my feeding rate values (as far as % body volume consumed) would be much reduced.

Aside from analytical variability there is also the problem of the variability in the tintinnids themselves. For example, what of the past physiological history of the tintinnids used in the experiment? It is not known whether the tintinnids were well-fed in the wild or on the brink of starvation. Blackbourn pointed out that tintinnids starved for >48 hours had difficulty eating when food was again offered to them and that digestion occurred more rapidly in well-fed than in starved tintinnids. The tintinnids used in my experiments remained unfed for 2-7 hours before the start of the experiment. Perhaps hungry (but not starving) tintinnids reach very high

levels of food consumption.

It is possible that tintinnids increase their rate of food consumption immediately before cell division and it is possible that they may not feed at all during the actual process of division. No attention was paid to reproductive state during this study (although tintinnid abundance did not change during the experiments), so this is a factor which deserves more attention.

It is not known whether tintinnids are continuous feeders in their natural environment. Goulder (1973) found no diel fluctuations in the number of food organisms inside the ciliate Loxodes over a 24 hour period and concluded that their grazing rate was constant. Blackbourn found no difference in the number of food cells contained in Tintinnopsis subacuta at dawn and dusk, and light intensity did not affect feeding rates. He also found that his tintinnids moved toward the water surface at all light levels. However, T. parvula in the North West Arm obviously migrate away from the light (as deep as 12 m) to areas of much reduced food levels, so they may in fact feed discontinuously. Others (Zaika and Ostrovskaya 1972 and Vitiello 1964) reported extensive vertical migrations (up to 50 m) by tintinnids. Whether this is merely a phototactic response or a response to food is unknown but migration into a nutrient-poor layer must affect feeding rates. All of my feeding experiments were carried out in the dark, which, again, may tend to maximize rates for the species concerned.

Blackbourn stated that larger tintinnids have a higher feeding rate than smaller tintinnids. I have not found this to be particularly true as regards Helicostomella subulata, Tintinnopsis parvula and Parafavella gigantea but the discrepancy may be more a result of activity rather than size, or even a combination of the two. For example, T. parvula carries a small but heavy lorica, the animal almost filling the lorida. Its movement can be described as nothing short of frantic. Thus it probably requires a rather substantial amount of food to meet its energy requirements. H. subulata is a rather small animal in a rather large but lightweight lorica. Its movement is determined and swift, hence a requirement for food perhaps similar to T. parvula. P. gigantea possesses an extremely large lorica with a proportionally large animal (as compared with Helicostomella). Its hexagonally-sculptured lorica has been suggested to be rather buoyant (Zeizschel 1967). Its movement is best described as leisurely, hence perhaps a lower food requirement is typical of this animal.

Figures 26-30 present histograms of the number of Rhodomonas lens inside various tintinnid species after one hour of feeding. In all except T. karajacensis and H. subulata only one or two food organisms were found. But this tells us nothing of the handling time of the organism; i.e., how fast they are digested and replaced. Hamilton and Preston (1969) reported that Uronema (a marine bactivorous ciliate) could

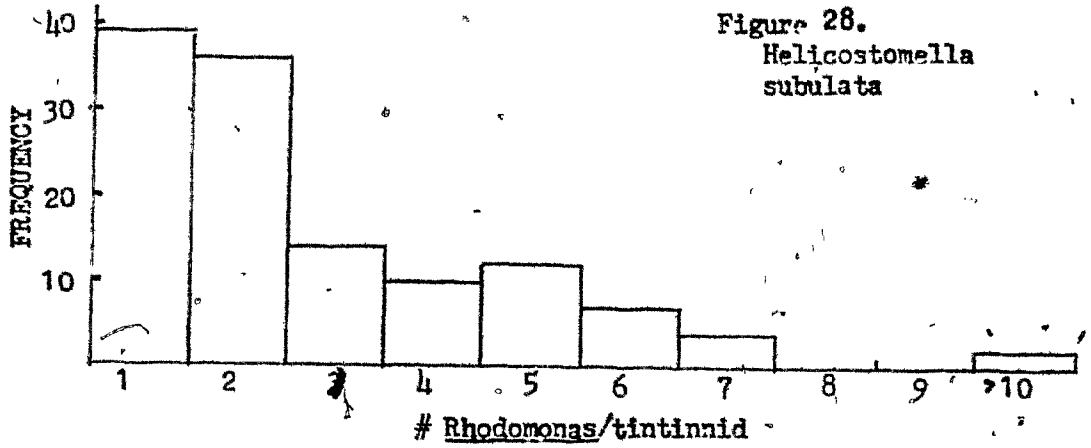


Figure 28.
Helicostomella subulata

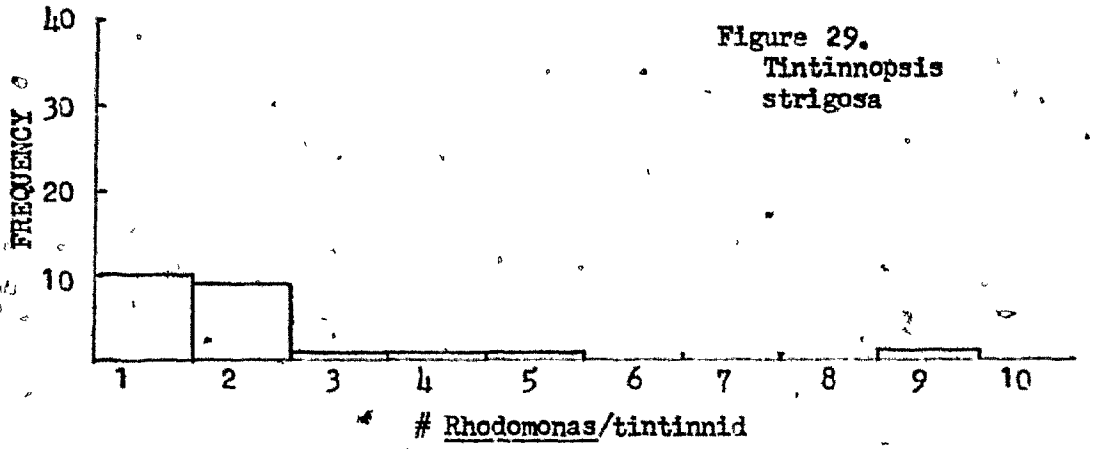


Figure 29.
Tintinnopsis strigosa

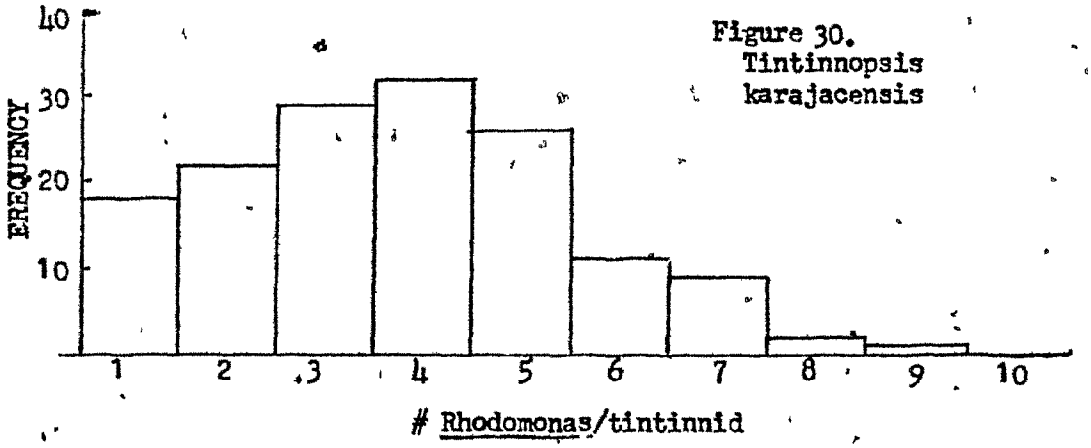


Figure 30.
Tintinnopsis karajacensis

form feeding vacuoles at the rate of one every 1-2 minutes, the contents of which were digested in as short a time as 30-45 seconds. One of their figures showed a Uronema with >50% of its volume occupied by food vacuoles. It is possible that tintinnids may also have a very high food turnover rate.

Tintinnids may have a preference for a certain type of food, a preference based on food size, shape, biochemistry, or a combination of these. Tintinnids probably do not eat many diatoms because even the smallest (like Skeletonema costatum) usually occur in chains and are hence too bulky for tintinnids to handle. Spittler's determination that tintinnids prefer live algal cells of between 2 and 20 μ diameter has already been mentioned. I have been unable to culture tintinnids on either diatoms or dinoflagellates but have been successful using a mixture of the flagellates Dunaliella, Isochrysis, Rhodomonas and Platymonas. Gold (1966, 1968, 1969a) has used these algae as well as the dinoflagellates Peridinium trochoidum and Glenodinium foliaceum for culturing tintinnids. From this study it appeared that H. subulata and T. parvula (and also P. gigantea--see Appendix B, Fig. 19) all eat Dunaliella, Isochrysis and Platymonas (H. subulata also consumed Rhodosorus and Pyramimonas). None seemed to thrive on Rhodomonas (except T. karajacensis). H. subulata seemed to avoid Monochrysis and it is interesting to note that Blackbourn's H. kiliensis also seemed to dislike Monochrysis, although his T. rapa, T. subacuta and T. parvula

consumed quantities of it. Dunaliella was also readily accepted in Blackbourn's experiments, except for T. rapa, for which it was probably too large. Rapport et. al. (1972) also found that Stentor coeruleus preferred to eat protozoa rather than algae. Slightly different tastes in food may in fact permit several tintinnid species of the same genus to co-exist in the same volume of water.

Assuming, then, that my values are acceptable, it is possible to calculate roughly whether tintinnids exert a control on nanoplankton blooms. During 1 July-12 October 1975, there were an average of 4400 Helicostomella subulata/l in the North West Arm. From Table 2, each Helicostomella could eat on the average 22 Dunaliella-size particles/hr or about 530/day (if it eats all the time). Thus the tintinnid population could consume about 2.3×10^6 algal cells/l/day. Most of the tintinnid blooms (>2000 tintinnids/l) occurred soon after or while the nanoplankton population was about 2×10^6 cells/l. The enormous 1972 summer tintinnid outburst (72,750 tintinnids/l) occurred soon after the nanoplankton reached a concentration of 16.4×10^6 cells/l.

Table 16 presents the tintinnid concentration, nanoplankton concentration and the estimated nanoplankton consumption by the tintinnids for four successive sampling dates during 1972. I propose that between 12 July and 26 July the tintinnids took advantage of the enormous food supply, quickly ate enormous amounts of it and were able to reproduce so rapidly

Table 16. Theoretical nanoplankton consumption by tintinnids

SAMPLING DATE	TINTINNID CONCENTRATION (#/l)	NANOPLANKTON CONCENTRATION (#/l)	ESTIMATED CONSUMPTION BY TINTINNIDS (# OF NANOPLANKTON CONSUMED/TINTINNID POPULATION/l/DAY)
14 June	1,075	1.1×10^6	0.6×10^6
28 June	1,730	5.3×10^6	0.9×10^6
12 July	6,377	16.4×10^6	3.4×10^6
26 July	72,750	3.4×10^6	38.5×10^6

that overpopulation so depleted the food supply as to cause rapid starvation and decline of the tintinnid population. It is most likely that this sequence of events was responsible for the rapid increase and decline in the abundance of tintinnids observed both in the North West Arm and in the Tower Tank. Both Prakash (1963) and Needler (1949) have found species of Favella to be responsible for the demise of Gonyaulax populations in natural waters. In short, tintinnids certainly feed at sufficient rates to enable them easily to control natural blooms of nanoplankton.

Finally, later sections will deal with observed growth rates of tintinnids in culture and in nature, and by way of intercomparison an attempt will be made to translate the feeding experiments into terms of possible growth rates, although the results obviously will be variable and subject to all the qualifications that have been stated.

Referring back to Fig. 25, the largest frequency of food volumes consumed was in the range of 0-10% of the animal volume per hour. We will assume an assimilation efficiency of 80% of the food consumed, a figure commonly used in such computations; further that the growth efficiency is 20% of the assimilated food, which probably is reasonable for small animals. Then a 5% consumption would lead to an increase of biomass of 0.8% per hour, which is equivalent to a doubling time of slightly more than 5 days.

The average consumption as shown in Fig. 25 is 24%, and a similar calculation indicates a doubling time of 26 hours. The maximum observed feeding rates bring the doubling time down to about 8 hours.

Later work on growth of cultures will suggest that the feeding rate is average or less than average; i.e., doubling times in excess of one day, but as suggested earlier, natural populations occasionally have been observed to increase more rapidly than this, a result that is not inconsistent with the maximum feeding rates that have been observed.

NITROGEN EXCRETION BY TINTINNIDS

INTRODUCTION

At least since the time of Harris (1959) it has been realised that marine nitrogen budgets did not balance; i.e., that phytoplankton appeared to require more nitrogen than was being supplied to them via bacterial decomposition and physical transport. It was suggested that zooplankton (usually copepods) were directly supplying the extra nutrients via their excretion. However, now that excretion rates by copepods are becoming known (Smith 1975), the nitrogen budget still does not balance. This discrepancy has led some (Johannes 1965) to suggest that marine protozoa may play an important role in nutrient regeneration in the sea, particularly since they numerically dominate the zooplankton at times (at least in summer) and are most abundant in the euphotic zone.

Little is known about nitrogen excretion by marine protozoa, most likely because of the technical difficulties involved in such investigations. Until recently analytical methods were crude and insensitive. It has been difficult to obtain sufficient numbers of these generally small organisms in order to obtain reliable results even with improved analytical techniques. The use of natural populations involves tedious isolation of individual animals. Cultures require feeding and there is then the problem of separating food from protozoa.

These problems are particularly acute with tintinnids, which resist culture and are destroyed by even the gentlest of filtration or centrifugation.

There have been a few quantitative estimates of nitrogen excretion by some protozoans. Table 17 lists some of the

Table 17. Previous investigations of nitrogen excretion by protozoa

PROTOZOAN INVOLVED	AMMONIA EXCRETION (μM·ammonia-N/animal/hour)	UREA EXCRETION (μM urea-N/animal/hour)	SOURCE
Didinium	2.29×10^{-1}	0	Weatherby (1929)
Paramecium	0	9.30×10^{-3}	"
Spirostomum	0	2.20×10^{-3}	"
Glaucoma	8.90×10^{-4}		Doyle and Harding (1937)
Tetrahymena	5.04×10^{-5}	3.62×10^{-5}	Nardone and Wilber (1950)
Paramecium aurelia	4.91×10^{-7}		Soldo and Wagtendonk (1961)

results (which I have calculated from the original data in order to make the values comparable to one another) of these investigations done with cultures of freshwater organisms. These studies prompted me to try to determine the nitrogen excretion rates of some tintinnids, abundant members of the summer zooplankton in the North West Arm.

METHODS

Because of the difficulties involved in the culture of tintinnids and in separating them from their food, I decided to use natural populations. The tintinnids were collected

either off the Oakland Pier or at Station E using a 30-cm diameter, 10 μ mesh net. The sample was returned to the laboratory and animals were isolated from it by means of a drawn-out pipette under a dissecting microscope. In this manner, for ammonia analysis, the animals were transferred into 150 ml of glass fiber filtered surface seawater (200 ml in the case of urea analysis) obtained at the same time and location as the net tow. The sample bottle and a control bottle containing the same amount of water but without tintinnids were wrapped in aluminum foil and placed in a cabinet in a 10° C cold room and left undisturbed for 9 hours. At the end of the incubation period, control and sample bottle contents were filtered through glass fiber filters and ammonia (Solorzano 1964) or urea (McCarthy 1970) analyses were performed on the filtered water.

Experiments were also run to determine whether tintinnids excrete amino acids. Collection of tintinnids was as above. Animals were isolated into 15 ml of filtered seawater in screw-top test tubes. The tubes were wrapped in aluminum foil and left undisturbed for 8 hours in a 10° C cold room. Amino acid analysis (using L-arginine as a standard) was done by T. Hollibaugh using a method developed by Zika (personal communication). In all experiments, an initial sample of seawater was analysed for ammonia, urea or amino acids in order to determine ambient concentrations.

RESULTS

Tintinnids do not appear to excrete (or take up) amino acids. The results of the ammonia and urea analyses are presented in Table 18. The average ammonia excretion was 6.65×10^{-6} µM ammonia-N/animal/hour. The average urea excretion was 4.43×10^{-6} µM urea-N/animal/hour. It appears that Helicostomella excretes larger amounts of ammonia than urea and that ammonia production is inhibited at higher concentrations of animals. Tintinnopsis appears preferentially to excrete urea.

DISCUSSION

Values obtained in this study were rather different from those of earlier studies. In general, the present values were lower. However, Soldo and Wagtendonk (1961) reported even lower values. Since their experiments ran for 12 days, it is assumed that their cultures were fed and that uptake by the food organisms might account for the low values. Higher values in the older studies were most probably the result of crude methodology. On the other hand, it is possible that such a wide range of values is real and a result of species differences in excretion rates.

The present values also seemed quite variable (especially for ammonia), the reasons being unclear at this time. Analytical precision was good, which provides confidence in the analytical method. There is no way presently to evaluate

Table 18. Nitrogen excretion by tintinnids

LATE (1975)	AMMONIA EXCRETION IN µM ammonia-N/ animal/hr	UREA EXCRETION IN µM urea-N/ animal/hr	KIND AND #/l OF ANIMALS INVOLVED (ANIMAL VOLUME IN μ^3)				
			HELICOSTOMELLA SUBULATA (18277)	TINTINNOPSIS PARVULA (24103)	T. STRIGOSA (26080)	T. SACCULUS (35614)	PARAFAVELLA GIGANTEA (389010)
3 Sept	3.0×10^{-6}		5800				500
10 Sept	6.9×10^{-6}		11200				
16 Sept	6.4×10^{-6}		2500	600			
21 Sept	13.2×10^{-6}		7200	100			
22 Sept	8.4×10^{-6}		7400				
23 Sept	11.7×10^{-6}		6800		200	100	
8 Oct	1.9×10^{-6}		2100	6600			
9 Oct	1.7×10^{-6}		1400	5200			
27 Aug		3.8×10^{-6}	4400				
11 Sept		6.1×10^{-6}	2300	200			100
15 Sept		2.6×10^{-6}	5900	300			
10 Oct		5.2×10^{-6}	300	5700			

the effects of mechanical manipulation of the animals but it is recognized that such manipulation could affect the results. On the other hand, this high variability in tintinnid excretion may be yet another (and at this time unexplainable) part of the trademark of variability as reflected in their variable abundance and variable rate of food consumption (Blackbourn 1974). Decrease in excretion with increasing animal density is not a new phenomenon. Hargrave and Geen (1968) reported it for phosphorus excretion by copepods and listed as possible causes physical interference, social effects and accumulation of excretory products.

There has been some controversy as to whether or not ciliates excrete urea. The present study indicates that tintinnids, at least, do. Weatherby (1929) found urea excretion in Paramecium and Spirostomum. Lwoff and Roukhelman (1926) did not find it in Tetrahymena, nor did Dewey, Heinrich and Kidder (1957). However, Nardone and Wilber (1950) did find urea excretion by this organism, at least in the early stages of growth. The Paramecium aurelia cultures of Soldo and Wagtendonk (1961) also failed to produce urea. Seaman (1954) said that Tetrahymena contains the enzymes of the ornithine cycle and can synthesize urea from ammonia and then convert this to ammonia again via a pH-sensitive urease. The value of such a biochemical tactic is unclear unless such an ability to inactivate ammonia is of value to animals living in confined spaces or in areas of high animal density. This suggestion is plausible when applied to tintinnids, confined to loricae.

It may be that the tintinnids in my experiments produced urea earlier in the experiment and produced little urea later on; hence my values may be underestimates (and the ammonia values overestimates if the urea were converted to ammonia during the 9-hour incubation). On the other hand, tintinnids may not produce urea until the level of ammonia in their micro-environment (i.e., inside their loricae) becomes somewhat toxic.

There is also the possibility that different protozoan species excrete different nitrogenous products (Cunningham and Kirk 1941). It is generally believed, for example, that there are basic differences between the arenaceous-loricate tintinnids (like Tintinnopsis) and hyaline-loricate forms (like Helicostomella). The tendency toward urea excretion by Tintinnopsis may be a manifestation of these differences. Perhaps the hyaline loricae are more conducive to ammonia diffusion than the more sturdily built Tintinnopsis loricae, making a less toxic form of nitrogen excretion necessary for the latter. Tintinnopsis also fits more snugly into its lorica than does Helicostomella and thus has less open space into which it can excrete.

Ikeda (1974) estimated the excretion rate of ammonia for an average zooplankter (E: μM N/animal/hr) using its individual body weight (W: mg dry weight/animal) and its habitat temperature (T: ^{o}C) in the following equation: $\log E = (-0.0094T) \log W + (0.02836T - 1.3664)$. For Helicostomella ($T = 10^{o}$ C; $W = 2.38 \times 10^{-6}$ mg) the predicted value is 5.71×10^{-6} μM N/animal/hr, which is in fair agreement with the experimental value of

6.65×10^{-6} µM N/animal/hr.

Continuing the "intercalibration" of experimental methods, the preceeding section on feeding rates was used to estimate possible doubling times of the population and can also be translated, with some simplifying assumptions, into projections of nitrogen excretion which can be compared with experimental data on this subject. The earlier analysis assumed that assimilation was 80% of total consumption and that the increase in biomass was 20% of assimilation, or 16% of total consumption. This much of the nitrogen content of the food, assuming a similar elementary composition, will be withdrawn into the formation of new tissue, and the remainder will be excreted in one form or another. The most likely source of soluble nitrogen is the assimilated fraction, which will be 64% of the total nitrogen consumption. The maximum value would be 84%, if all nitrogen consumed is converted to ammonia and urea, but this seems unlikely. Since the mean excretion observed in the experiments is 2.79 µg-at/mg dry weight in an hour (= 39.06 µg N/mg dry weight/hr), the estimated total consumption is 47-61 µg N/hr. However, this is a very rough estimate in view of the fact that experimental values for nitrogen excretion were highly variable.

Approaching the problem from the opposite viewpoint, and assuming that the nitrogen content of the nanoplankton food is about 6%, the experimentally observed feeding rates lead to an estimate of nitrogen consumption of 3-45 µg N/mg dry weight/hr with a mean of 14.4 µg N.

The agreement clearly is not good. The high end of the estimate based on feeding rates overlaps with the lower range of experimentally determined excretion rates but the averages differ by a factor of at least four. It is possible that increased bacterial activity in the experimental bottles as a result of the presence of the animals themselves may have produced an added amount of ammonia, but the quantitative contribution of the bacteria is unknown. However, due to reduced temperature and relatively short incubation time, this contribution is not thought to be large. It is extremely difficult to make an accurate assessment of the role of tintinnids in general nitrogen balance until the reasons for the discrepancy have been discovered, and yet the information now available is an improvement over the complete lack of knowledge that existed prior to these experiments.

Assuming that the present values are plausible, a few simple calculations reveal some insight of the role of tintinnids in nutrient regeneration. For example, on the average there were 4400 Helicostomella/l in the North West Arm during the period 1 July-12 October 1975 excreting on the average 6.65×10^{-6} µM N/animal/hr into the water, which represents an input of 0.696 µM N/l/day or 696 µM N/m^3/day. In Bedford Basin, a part of Halifax Harbour a few miles away from the NWA (and being similar to the NWA in phytoplankton and protozoan communities), the primary production during the period 1 July-15 October averages about 100 mg C/m^2/hr. Assuming a

depth of NWA Station E of 12 m and a similar primary production, this amounts to about 200 mg C/m^3/day or 16.67 mM C/m^3/day. Assuming a C:N ratio of 6.625, this represents a nitrogen requirement for the phytoplankton of 2516 µM N/m^3/day. Therefore, the tintinnid population alone could supply 25-30% (27.7%) of the nitrogen requirement of the phytoplankton.

Helicostomella, without their loricae, possess an average volume of 18,277 μ^3. Assuming a density of 1.00 for cell contents, then 1 $\mu^3 \approx 10^{-6}$ µg wet weight. Assuming further that dry weight ≃ 13% of the wet weight, then one Helicostomella represents 2.38×10^{-3} µg dry weight. Again, with an average of 6.65×10^{-6} µM N excreted/animal/hr, an excretion rate of 6.71×10^{-2} µM N/µg dry weight is obtained. Calculations from data given by Harris (1959) yield a value of 2.87×10^{-3} µM N/µg dry weight/day for mixed zooplankton (primarily Acartia). Calculations from Smith's (1975) data on Centropages typicus yield a value of 5.95×10^{-4} µM N/µg dry weight/day. Even considering that not all the dry weight of a copepod is of metabolically active material, excretion by tintinnids may be one to two orders of magnitude higher than excretion by macrozooplankton. These data seem to parallel those of Johannes (1965) which revealed that on a per weight basis, marine protozoan phosphate excretion was one to two orders of magnitude greater than marine microcrustaceans and several orders of magnitude higher than marine macrofauna.

Table 19 represents protozoan biomass and protozoan excretion estimates during the four Scotian Shelf cruises. It

Table 19. Average protozoan biomass (PB: mg dryweight/m^3) in the top 50 m of the water column and their estimated nitrogen excretion (E: ng-at N/l/day) during the four Scotian Shelf cruises.

	MAR(SSIII)		JUNE(SSI)		AUG(SSIV)		NOV(SSII)		$\bar{X}$	
STAT. #	PB	E	PB	E	PB	E	PB	E	PB	E
1	2.79	38.17	3.36	45.96	22.67	310.13	8.17	111.77	9.25	126.51
2	2.41	32.97	4.53	61.97	15.08	206.29	6.27	85.78	7.07	96.75
3	2.59	35.29	4.13	56.50	9.74	133.24	5.09	69.63	5.39	73.65
4	2.83	38.71	3.65	48.79			3.78	51.71	3.42	46.40
5	1.67	22.85	2.79	38.17	21.41	292.89	7.68	105.06	8.39	114.74
6	3.32	45.41	6.12	83.72			4.66	63.75	4.70	64.29
7	1.53	20.93	9.59	131.19	14.43	197.40	9.55	130.64	8.78	120.04

Table 20. Comparison of protozoan (PB) and macrozooplankton (ZB) biomass (mg dry weight/m^3); protozoan (PE) and macrozooplankton (ZE) nitrogen excretion (ng-at/l/day); and protozoan N excretion:phytoplankton N assimilation (PE:PA) and macrozooplankton N excretion:phytoplankton N assimilation (ZE:PA) ratios for selected stations during the four Scotian Shelf cruises.

MONTH	STA. #	PB	ZB#	PB:ZB	PE	ZE*	PE:ZE	PA*	PE:PA	ZE:PA*
MAR	3	2.59	12.2	0.21	35.29	2.2	16.04	31.6	1.12	0.07
SSIII	4	2.83	7.2	0.39	38.71	2.3	16.83	132.7	0.29	0.02
JUNE	2	4.53	34.0	0.13	61.97	16.0	3.87	31.7	1.95	0.50
SSI	3	4.13	25.0	0.17	56.50	17.3	3.27	40.6	1.39	0.42
	5	2.79	86.0	0.03	38.17	16.2	2.36	68.2	0.56	0.24
AUG	3	9.74	72.4	0.13	133.24	45.8	2.91	151.9	0.87	0.30
SSIV	7	14.43	7.6	1.90	197.40	7.3	27.04	57.2	3.45	0.13
NOV	3	5.09	36.8	0.14	69.63	9.7	7.18	171.1	0.41	0.06
SSII	4	3.78	15.7	0.24	51.71	13.3	3.89	49.3	1.05	0.27
	$\bar{X}$	5.55	33.0	0.37	75.85	14.5	9.27	81.6	1.23	0.22

* data from R. O. Fournier
PB average biomass in the top 50 m of the water column
ZB average biomass for the entire water column
ZE average value for the euphotic zone

is based on the following assumptions:

(a) an average Strombidium has a volume of 19,272 μ^3

(b) other protozoa (including tintinnids without their loricae) have an average volume of 35,767 μ^3

(c) protozoan cell contents have a density of 1

(d) dry weight $\approx$ 13% wet weight

(e) protozoan excretion rate $\approx$ 0.57 µg-at N/mg dry weight/hr. This value is the minimum determined from experiments with NWA tintinnids, all experiments being carried out at 10° C, thus assuming a lower excretion rate for oceanic protozoa.

Table 20 compares protozoan biomass and excretion. Although it would not ordinarily be acceptable to compare the protozoa in the top 50 m with the zooplankton in the entire water column, the fact that the vast majority of the protozoa is concented in the top 50 m makes this a reasonable procedure. It is clear from these calculations that the protozoa could contribute significantly to the nitrogen content of the water on the Scotian Shelf. In summer the protozoan biomass may exceed that of the macrozooplankton. Their contribution to the nitrogen cycle is an order of magnitude greater than that of the macrozooplankton. The protozoa seem to be able to supply more nitrogen than the phytoplankton require, which of course is theoretically impossible. Various possibilities for error exist:

(a) underestimating the excretion rates of the macrozooplankton

(b) underestimating the assimilation of the phytoplankton

(c) overestimating the protozoan biomass

(d) temperature effects

(e) protozoa not continually eating and excreting

(f) failure to take into account possible differences between NWA tintinnids and Scotian Shelf protozoa (overestimating excretion rates).

There is no evidence to support the first two. The protozoan biomass estimates are probably conservative. In measuring the length of tintinnids, for example, I disregarded the membranelles and the pedicel.

It is likely that the values for March and June are overestimates because the water temperature on the Shelf then was only 3° C. On the other hand, the August values are underestimates since the Shelf water temperature then was 17-21° C. November values, when the water temperature was 9° C should then be comparable with the experimental values.

The last of the possibilities is probably the most valid criticism. The abundance of phytoplankton on the Shelf is much less than in the NWA so the protozoa may not be as well fed and may not excrete as much as in the NWA. We do not know, for example, if ill-fed animals are able to achieve a higher assimilation rate of the food which they are able to obtain, but this would not change the results very much. However, with a lesser abundance of available food, food consumption may lie near the lower end of the range described in Section 5, with

correspondingly lower excretion. If we use the excretion value of 0.18 µg-at N/mg dry weight/hr obtained from a food intake of 3 µg N/mg dry weight/hr (the latter value being derived from the feeding data), then the contribution of the protozoa to the nitrogen cycle of the Scotian Shelf would be considerably reduced and perhaps more realistic. Again, it should be emphasized that these determinations are rough ones and more work in the field of protozoan excretion (especially in open oceanic areas) will be necessary before the issue can be resolved. Also, we do not know how much protozoan excretion occurs in the euphotic zone as opposed to how much is excreted below this zone. If a significant amount is liberated in the lower part of the water column, the rate of nutrient cycling between phytoplankton and protozoa would be reduced.

As a final note, on the August 1975 Scotian Shelf cruise few excretion estimates of macrozooplankton could be made due to the sparseness of animals in the area at that time. However, protozoan concentrations were commonly greater than 10,000 individuals/l in the upper 50 m of the water column. The phytoplankton at this time was completely dominated by very small (<20 µ) forms. Intuitively, then, given these high cell numbers and high excretion rates, it is likely that protozoa must play an important role (at least in summer) in nutrient regeneration in coastal marine areas.

7. SOME OBSERVATIONS ON POPULATION GROWTH AND REPRODUCTION OF TINTINNIDS

INTRODUCTION

The erratic abundance of tintinnids must be partly a result of their reproductive rates. However, few determinations have been made of these rates and all of the determinations have been made with cultures of tintinnids. For example, Gold (1970, 1971) has reported doubling times of 26 hours for Metacylis and 2.5-6 days for Tintinnopsis beroidea. Beers and Stewart (1970) reported that Favella serrata populations doubled in 24 hours at 18° C in their lab, and they suggested that a general doubling time for tintinnids would be 48 hours. I have been able to culture several NWA tintinnid species and have thus been able to estimate their reproductive rates, which are reported here.

On the other hand, cultures do not always reflect the conditions found in the field. Lack of predation and abundant food supply in cultures may shorten reproductive times while absence of a vital nutrient or presence of an unsuitable food source may lengthen reproduction times. Ideally, what is desired is a method for estimating the reproductive state and rate of natural populations. For tintinnids, many of which possess agglomerated or arenaceous loricae, it is not easy merely to note the number of animals undergoing fission in any given population.

It has been noted by several workers (Hofker 1931, Biernacka 1965 and Burkovsky 1973) that many tintinnid species (and perhaps all of them) are able to add material to their loricae and thus lengthen them throughout the life of the animal (This fact, incidentally, makes lorica length a very poor taxonomic characteristic.). Gold and Morales (1974a) have pointed out that there are obvious differences between juvenile loricae and loricae from past generations and that these differences might be used to study population growth in the natural environment.

Gold (1974a) has carefully studied tintinnid loricae during 6-8 day blooms of Tintinnopsis acuminata, T. dadayi and Tintinnidium fluviatile in Eel Pond, Woods Hole. He noted the following "events" which correspond to similar events found in tintinnid cultures: I. an increase in the percentage of long loricae followed by an abrupt replacement by shorter loricae (equivalent to the lag phase in culture); II. disappearance of long loricae and linear increase in shorter loricae (equivalent to log phase in culture); III. the reverse of II (equivalent to stationary phase in culture). I have attempted to determine population growth rates using loricae lengths for several NWA tintinnid species, particularly Helicostomella subulata, which undergoes several population peaks and declines during the 3-4 months it is found in the NWA.

Although the usual mode of reproduction among tintinnids is binary fission, several species have been observed to undergo

conjugation (Bresslau 1906, Entz 1909, Apstein 1895 and Silva 1950). I have observed apparently conjugating pairs of Tintinnopsis parvula and will discuss some of the aspects of the process.

Finally, because the presence of certain tintinnid species seems to be an annual event of limited duration, the question arises as to what happens to them when they disappear from the area. Tintinnid cysts have been reported by Biernacka (1952) and Zeitzschel (1966) who suggested that cyst formation enables tintinnids to withstand unfavourable conditions. Wailes (1924, 1943) reported the occurrence of spores in Helicostomella subulata. I have observed what appear to be cysts among several tintinnid species but I question the existence of spores.

METHODS

During summer 1974 I had some success in culturing several tintinnid species--Tintinnopsis sacculus, T. strigosa, T. karajacensis and Helicostomella subulata. They would not grow at 2° C but would grow at 10° C on a 16 hour light-8 hour dark cycle. The animals would not grow on unialgal cultures of Isochrysis, Monochrysis, Porphyridium, Dunaliella or Amphidinium nor would they grow on a mixture of these, although T. karajacensis was ultimately grown on a mixture of Rhodomonas, Platymonas, Dunaliella and Isochrysis. Best growth was obtained by feeding tintinnids on a mixture of unidentified nanoplankters isolated from the NWA. Tintinnids seemed to grow best in f/2 medium (in Stein 1973) but limited success was also

achieved with Gold's (1968) D medium. I was not able to subculture any of the species.

In order to assess the value of lorica length measurements as an indicator of the reproductive state of natural populations, I measured 30 randomly selected H. subulata loricae every day during the period 10 July-23 August 1975. Measurements were also made on six other species, although not quite on so regular a basis. These measurements were related to population abundances.

On 20 March 1975 I sampled the sediment at Station E in the NWA using a small snapper grab. 0.5-ml samples of the sediment were observed using an inverted microscope in order to determined whether tintinnid cysts might be found in the sediment.

RESULTS

Figure 31 shows growth curves for T. sacculus, which are typical of the observed population growth in culture, and data for other species are illustrated in Appendix D, Figs. 1-3. Appendix D, Figs. 4-7 show both the average lorica length and the abundance of natural populations of H. subulata, T. sacculus, T. parvula, T. strigosa, Parafavella gigantea, T. karajacensis and Leprotintinnus pellucidus. Note the following features of the growth curves: (a) the rather long lag; (b) the exponential increase in numbers; (c) the even more rapid decline in the populations.

Figure 31. Population growth of Tintinnopsis sacculus in culture.

Figure 31.

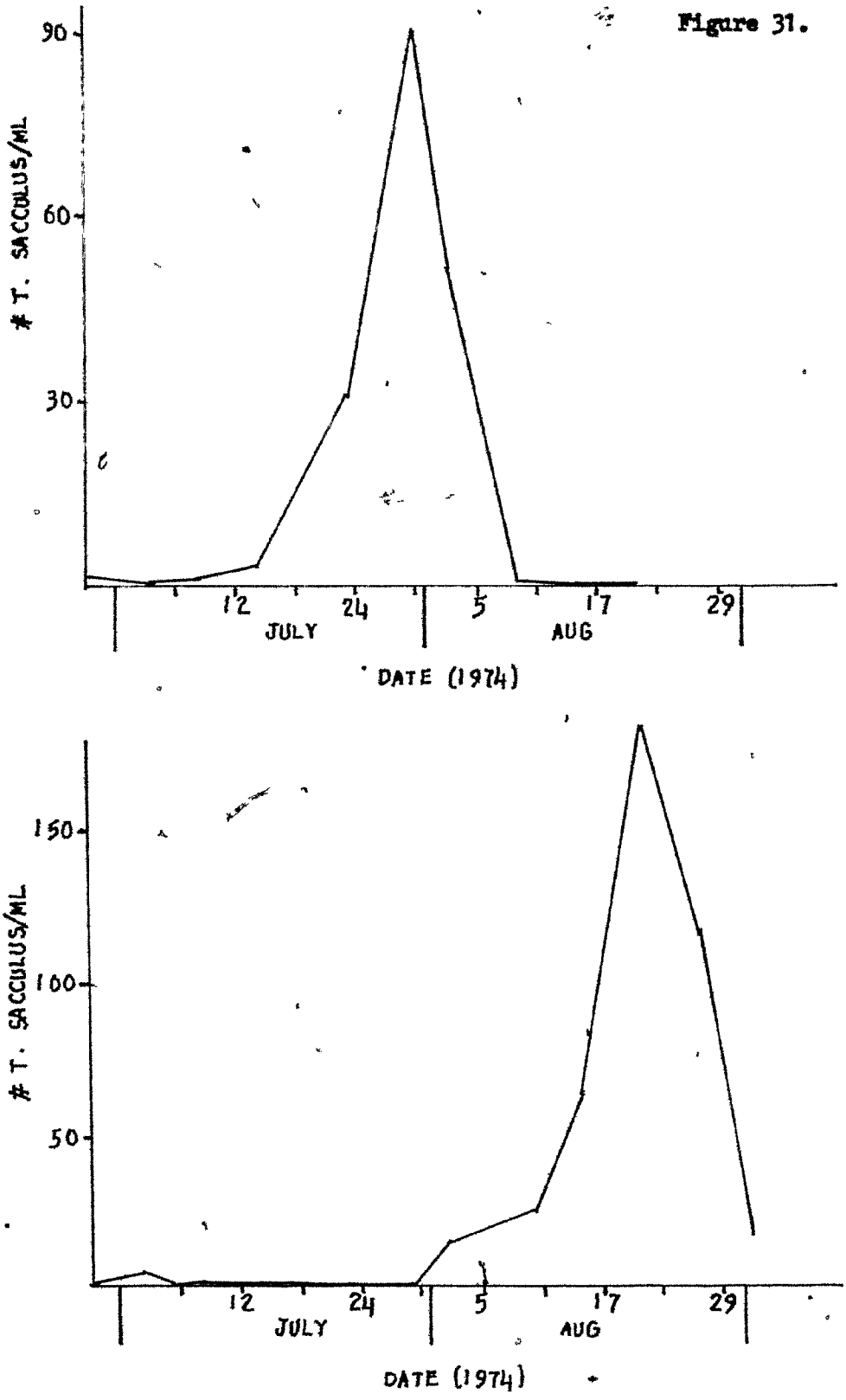

90
60
30
T. SACCULUS/ML
12
24
5
17
29
JULY
AUG
DATE (1974)
150
100
50
T. SACCULUS/ML
12
24
5
17
29
JULY
AUG
DATE (1974)

Table 21 presents population doubling times in days as inferred from (a) cultures, (b) times between peaks on the NWA abundance curves and (c) times between troughs on the lorica length curves. This last measurement is based on the hypothesis that quickly reproducing populations produce shorter loricae because there is not enough time between divisions for the loricae to grow longer.

Table 21. Population doubling times (in days) inferred from (a) cultures (b) population abundance and (c) lorica length

SPECIES	CULTURE	ABUNDANCE	LORICA LENGTH
H. subulata	3	2-8	2-6
T. sacculus	3-5	4-5	5-7
T. parvula	-	4	3-7
T. strigosa	3-9	3-6	2-6
P. gigantea	-	2-8	3-7
T. karajacensis	1-2	4-6	5-6
L. pellucidus	-	4	3-7

Correlation between abundance and lorica length of Parafavella and Leprotintinnus was negative but barely significant (correlation coefficient of -0.55 and -0.54 respectively). Correlation for T. sacculus and for T. strigosa were also negative but not significantly so (-0.31 and -0.29 respectively). There was no correlation between abundance and lorica length for Helicostomella, T. karajacensis or T. parvula. It would appear from the graphs that the average lorica length of Helicostomella generally increased as the season progressed while that of T. sacculus generally decreased. Lorica length of T.

parvula and T. strigosa did not much change from their initial appearance until their decline despite several peaks during this time. Toward the end of their respective blooms lorica lengths of Parafavella and T. karajacensis tended to decrease while those of Leprotintinnus increased. There was also no significant correlation between the change in population abundance and average lorica length for any of the species.

Observations of tintinnids in culture have revealed that the animals (particularly the agglomerated forms) tend to lose the ability to produce loricae. For example, on 14 January 1975 a culture of Tintinnopsis tubulosoides was begun from a freshly-collected net tow off Coney Island, New York. Within a few days the loricae became more hyaline due to the lack of particles in the culture medium. The average lorica length at the time of collection was 86 μ. On 29 January the average lorica length decreased to 48 μ; on 5 Feb to 36 μ; and on 18 Feb to 27 μ. Such changes are represented in Appendix B, Figs. 20-24. In addition the percentage of non-loricate animals increased from 0% on 14 Jan to 26% on 29 Jan to 35% on 5 Feb to 59% on 18 Feb. Cultures of non-loricate tintinnids may remain viable for a short time but it has been my experience that such cultures die out rather rapidly.

Animals which appeared to be conjugating have only been observed among Tintinnopsis parvula which were observed in preserved samples during July and Sept-Nov (Appendix B, Fig. 10). No other species were observed in conjugation and the entire

process of conjugation was not observed, even in T. parvula. No attempt was made to determine the proportion of the population undergoing conjugation except on 15 Sept 1975 when 6% of the population appeared as conjugating pairs.

What appear to be cysts have been observed most often in Helicostomella (Appendix B, Fig. 25), occasionally in Leprotintinnus (Appendix B, Fig. 26) and once in Acanthostomella norvegica (Appendix B, Fig. 27). These cysts are somewhat amorphous structures surrounded by a thick wall. Staining with OsO_4 revealed large amounts of osmiophilic material, probably lipid. During 1975 Helicostomella cysts were first observed on 12 Aug and were seen regularly until sampling ceased on 12 Oct. Usually <1% of the loricae contained cysts except during 16-19 Aug and 4-12 Oct when about 3% of the loricae contained cysts. At most, 5% of the loricae contained cysts. Few cysts were observed during 29-Aug 9 Sept. Excystment was not observed, but Paranjape (personal communication) has observed cysts to development into normal Helicostomella some two months after encystment. Biernacka (1952) reported that the process of encystment takes about 6-8 hours to occur.

The sediment of the NWA at Station E consists of a fine mud (particle size <150 μ) which is very black and very foul. 99.9% of the loricae found were those of Tintinnopsis parvula in various stages of decomposition. No trace of a Helicostomella lorica was found nor was anything seen resembling a tintinnid cyst.

Spores similar to those pictured in sketches by Wailes

(1924, 1943) are shown in Appendix B, Figs. 28 and 29. These "spores" have never been observed to develop further and it is thought that they may in fact be a result of parasitic infection of the tintinnids. They were only observed in Helicostomella during August, the maximum number of animals being infected being 2.5% on 20 Aug 1975.

DISCUSSION

Cell numbers attained in culture were as great as and usually greater than those encountered in the field and the abundance may be near the limit attainable in batch culture. Gold (1970), however, has attained abundances of >1000/ml.

Certain features of the growth curves appear repeatedly with several species. The rather long lag period in my cultures may be a result of the following: (a) too few initial isolates (Note the reduced lag period for T. karajacensis when the initial number of isolates was quite high.); (b) overfeeding, which can lead to clogging of the membranelles; (c) adaptation to a new diet. The rapid increase in cell numbers may occur after some conditioning of the environment by the tintinnids. The rapid decline in the cultures parallels the same event in the field, but as was pointed out in a previous section, the demise of the cultured population is more probably due to a build-up of metabolic wastes rather than to predation, dispersion and food exhaustion which are the probable causes of population decline in the field. On the other

hand, it cannot be ruled out that tintinnids in general have a rather definite but ill-defined life span in culture as was noted by Webb and Francis (1969) for cultures of Stentor.

Fenchel (1968) presented a graph relating generation time of benthic ciliates (which ranged from 2.4-46 hours) to their body volume. Since the average body volume (excluding lorica) of tintinnids is about 10^5 μ^3, their generation time should be about 25 hours, which does not agree particularly well with my values. However, considering the unknown effect of the presence of the lorica and the fact that my cultures were grown at 10^0 C as opposed to Fenchel's work at 20^0 C (10^0 C is a more realistic environmental temperature, at least for tintinnids), then my values are probably realistic.

Generation times as inferred from cultures, natural abundances and lorica length are in fair agreement despite the lack of correlation between the latter two. What correlation there is may, in fact, be fortuitous, despite the apparently valid reasoning for the existence of such a correlation.

Reduction (or extension) of cell size (or lorica size) for one reason or another is fairly common. Gold's (1974b) work on the reduction of tintinnid lorica length during rapid reproduction has already been mentioned. During the January 1975 Tower Tank bloom the lengths of T. strigosa, H. subulata and T. karajacensis were 83, 172 and 84 μ respectively. NWA populations of T. strigosa, H. subulata and T. karajacensis had average lorica lengths of 87, 239 and 120 μ respectively.

Summers (1963) noted this same phenomenon in Tetrahymena pyriformis; i.e., during log phase there was a decrease in individual cell size and the cells were smallest at the end of log growth. Cell size increased during stationary phase. Summers also noted a decrease in cell volume with an increase in temperature. Gold (1974a) noted this phenomenon in tintinnid lorica length whose decrease at higher temperature he attributed to faster reproduction at higher temperatures. Burkovsky (1973) presented a series of lorica length vs. frequency curves for Parafavella denticulata, which showed a progressive lengthening of the loricae from summer to winter. These curves are remarkably smooth and it would be interesting to pursue this type of analysis with other species. Unfortunately, none of the NWA species is present all year.

Many planktonic organisms exhibit cold- and warm-water ecotypes--adaptations towards optimum area:volume ratios in water of different densities. If one wants to use lorica lengths to assess reproductive rates the question arises as to how one separates direct temperature effect on the lorica from the reproductive effect.

Other factors also confuse the relationship. The decrease in lorica-forming ability of tintinnids in culture has been mentioned, and the lorica size of several species declined toward the end of their residence times in the field. Hence, a decline in the lorica length may merely indicate the decline in the viability of the population as a whole rather than indicating increased reproduction.

Kimball, Caspersson, Stevens and Carlson (1959) pointed out that Paramecium aurelia decreased in size in a food-limited situation. How does one separate nutritional effects on size from reproductive effects?

What happens if predators selectively consume smaller forms--or larger forms? This, too, would interfere with the use of lorica lengths as an indication of reproduction rates.

Finally, the behaviour of certain tintinnids may also cloud the issue. For example, Hofker (1931) stated that some agglutinated species pile up matter around the oral opening just before division, thus lengthening the lorica. I have observed this phenomenon in T. parvula (Appendix B, Fig. 30) and in T. strigosa (Appendix B, Fig. 31). Thus, longer loricae rather than shorter loricae would be an indication of reproduction in these species. Also, in T. sacculus, the longest loricae often contain two individuals (Appendix B, Fig. 32) as if the new lorica is almost completely formed before the two individuals finally separate. Again, long loricae rather than short indicate reproduction.

In short, there are many difficulties with the lorica length method of assessing reproduction rates. However, a knowledge of individual species biology and a knowledge of population abundance may still enable us to use this method effectively in the field, particularly since tintinnids seem to do such anomalous things in culture.

The decrease in lorica size and the production of anomalous loricae in culture has been observed by Gold (1969b). The total loss of loricae in cultures has been observed by Gold and Morales (1974b). Although they were able to increase the number of loricate animals from 2% to 20% in some of their cultures by adjusting the temperature, the fact that non-loricate tintinnids are rarely found in nature and the unfailing demise of non-loricate tintinnid cultures indicate to me that loss of the lorica represents a manifestation of physiological distress and loss of viability.

A considerable amount has been written about tintinnid conjugation but the process remains rather obscure. Consider, for example, the gentle controversy as to how conjugation actually occurs. Bresslau (1906), Silva (1950) and I maintain that conjugation occurs in an oral end to oral end position in Stenosemella nucula, Tintinnopsis ventricosa and T. parvula respectively. Gold (personal communication) maintains that it occurs with the animals actively swimming side by side. Entz (1909) further clouds the issue by presenting Favella conjugating side by side, oral end to oral end and oral end to aboral end. Apstein (1895) wrote that he observed Tintinnus ampulla swimming in pairs side by side for several hours and concluded that they were conjugating. However, he also stated that Codonella lacustris conjugated in an oral end to oral end position. The objection has been raised that oral end to oral end conjugation does not allow the animals to swim during

the process. Other protozoa (Stentor, for example) become almost motionless during conjugation (Webb and Francis 1969) and I maintain that swimming would be a waste of energy during a rather critical period in the life of the tintinnid. If tintinnids are like other planktonic ciliates the process does not take long so sinking would not be too extensive. Sinking may not be important anyway in shallow neritic waters. Conjugation has not been reported for open oceanic species. I found the greatest number of T. parvula and the greatest number of apparently conjugating pairs just off the bottom at Station E in 1972 so they probably do sink. A non-swimming conjugating pair may be less noticeable to predators as it sinks into deeper and darker water. Finally, a closed oral end to oral end position perhaps provides a stronger bond than the open, free-swimming side by side position. I suggest that the tintinnids may separate and swim side by side for a time after the exchange of nuclear material has been completed. On the other hand, conjugation may occur in different ways depending on species.

An even more important question than how is why do tintinnids conjugate, besides merely to renew genetic viability. What initiates the conjugation process? Nothing is known about the factors influencing tintinnid conjugation. Webb and Francis (1969) pointed out that Stentor coeruleus cultures almost always exhibit conjugating pairs between the 7th and 18th day of their 30-day life span, suggesting that this is an inherently timed process. They also stated that conjugation

occurred during a decline in the food supply. Sonneborn (1939) found that Paramecium aurelia did not conjugate when overfed or completely starved. Giese (1939) believed that food supply was the most important factor in inducing conjugation in Paramecium multimicronucleatum. He found that a decrease in food supply following a period of plenty was required for conjugation. The process of conjugation and the factors affecting it in tintinnids are an area for further study.

Another pressing problem concerns where the tintinnids go when they are not in the plankton of a given area. Helicostomella subulata is a case in point. It is totally absent from December until May in the NWA. If it forms cysts, what happens to them? Why is there no trace of Helicostomella loricae in the sediment? They may be washed out to sea but Helicostomella is very rarely found in open oceanic areas and it seems clear that population growth in the NWA is initiated well within the NWA and is carried offshore. Zeitzschel (1966) believed that oceanic species formed cysts which remained in the loricae and floated while neritic species formed spores which sank. I found no evidence of either in the sample that was examined, but this hardly constitutes a thorough search. At the moment the question remains unresolved.

8. SUMMARY

1. The species composition, distribution and abundance of tintinnids and other protozoa were investigated during a four-year study of the North West Arm of Halifax Harbour, Nova Scotia, during a one-year study of the Scotian Shelf and during a two-week study of Nain Bay, Labrador.

2. Tintinnids in Canadian waters tend to occur with greatest abundance during summer and fall when their abundance may exceed 40 individuals/ml. During the rest of the year tintinnid abundance remains very low.

3. The presence of all species of protozoa is marked by huge variations in abundance over very short periods of time (i.e., less than one day).

4. Many of the species (especially the tintinnids) are very transient, appearing the disappearing very quickly (i.e., within a week).

5. During the occurrence of tintinnids in summer the phytoplankton is completely dominated by nanoplankters on which the tintinnids must certainly feed.

6. The oligotrichous strombidia are numerically much more abundant than tintinnids or any other group of protozoa but little is known about them. The gymnostomatid Cyclotrichium meunieri also often equals or exceeds tintinnid and strombidia

abundances but little is known about it either. The two most abundant tintinnids in the North West Arm are Helicostomella subulata and Tintinnopsis parvula.

7. The control of tintinnid populations in the field is most likely food supply modified by complex interactions with grazers, temperature, reproductive rates and perhaps even weather and the tides.

8. Tintinnids can consume from 0 to 75% of their body volume per hour when feeding on microflagellates.

9. Filtering rates of tintinnids feeding on microflagellates range from 0 to 5 µl per hour.

10. Helicostomella subulata can consume up to 50 Dunaliella, 170 Isochrysis, 11 Monochrysis, 46 Platymonas or 3 Rhodomonas cells per hour.

11. There is a positive correlation between abundance of nanoplankton and abundance of tintinnids in the field, and there are indications that tintinnids may easily control the abundance of natural populations of such small flagellates.

12. Tintinnids do not excrete amino acids but may excrete considerable quantities of ammonia (average rate of 6.65×10^{-6} µM ammonia-N/animal/hr) and urea (average rate of 4.43×10^{-6} µM urea-N/animal/hr). These rates are sufficient to supply 25-30% of the nitrogen requirement of the North West Arm phytoplankton and are one to two orders of magnitude higher than the excretion rates of marine macrozooplankton.

13. Reproductive rates of tintinnids range from 1 to 9 days, averaging 4 days. These rates were determined for cultures and also for field populations using abundances and lorica lengths as indicators of reproductively active populations.

REFERENCES

Apstein, D. 1895. Ein Fall von Conjugation bei Tintinnen. Schriften des Naturwissenschaft. Ver. Schleswig Hols. 10: 95-96.

Bary, B. M. and A. G. Stuckey. 1950. An occurrence in Wellington Harbour of Cyclotrichium meunieri Powers, a ciliate causing red water, with some additions to its morphology. Trans. Roy. Soc. New Zealand. 78: 80-92.

Beers, J. R. and G. L. Stewart. 1970. Numerical abundance and estimated biomass of microzooplankton. In: Strickland, J. D. H. (ed.), The ecology of the plankton off La Jolla, California, in the period April through September, 1967. Bull. Scripps Ins. Oceanogr. 17: 67-87.

Biernacka, I. 1948. Tintinnoinea in der Bucht von Danzig und den angrenzenden Gewassern. Poln. Biul. mursk. Inst. ryb. Gdyni. 4: 78-91.

Biernacka, I. 1952. Studies of the reproduction of some forms of the genus Tintinnopsis Stein. Ann. Univ. Marie Curie. Sklodowska 6(c):1-21.

Biernacka, I. 1965. Ausscheidung gehausebildender Substanzen durch reife Formen gewisser Arten der Gattung Tintinnopsis Stein. Acta Protozool. 3: 265-268.

Bigelow, H. B. 1924. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bureau Fish. 40: 1-509.

Bigelow, H. B., L. C. Lillick and M. Sears. 1940. Phytoplankton and planktonic protozoa of the offshore waters of the Gulf of Maine. Part I. Numerical distribution. Trans. Amer. Philos. Soc. 31: 149-191.

Blackbourn, D. J. 1974. The feeding biology of tintinnid protozoa and some other inshore microzooplankton. PhD Thesis. Univer. British Columbia. 227 pp.

Brandt, K. 1907. Die Tintinnodeen. Systematisher Teil. In: Ergebnisse der Plankton Exped. Humboldt-Stifung. 3: 1-499.

Bresslau, D. 1906. Eine Anzahl Tintinnen aus dem Plancton der Bucht von Rio de Janiero. Verhand. Deutsch. Zool. Gesellschaft. 16: 260-261.

Burkovsky, I. V. 1973. Variability of Parafavella denticulata in the White Sea. Zool. Zhurn. 52: 1277-1285.

Bursa, A. S. 1961. The annual oceanographic cycle at Igloolik in the Canadian Arctic. II. The phytoplankton. J. Fish. Bd. Canada. 18: 563-615.

Campbell, A. S. 1926. The cytology of Tintinnopsis nucula (Fol) Laackmann with an account of its neuromotor apparatus, division, and a new intranuclear parasite. Univ. Calif. Pub. Zool. 29: 179-236.

Campbell, A. S. 1927. Studies on the marine ciliate Favella (Jorgensen), with special regard to the neuromotor apparatus and its role in the formation of the lorica. Univ. Calif. Pub. Zool. 29: 429-452.

Campbell, A. S. 1954. Tintinnina. pp. D166-D180. In: R. C. Moore (ed.), Treatise on invertebrate paleontology. Part D. Protista. 3. Protozoa (chiefly radiolaria and Tintinnina). Geol. Soc. America.

Corliss, J. O. 1962. Taxonomic procedures in classification of protozoa. p. 37-67. In: C. C. Ainsworth and P. H. A. Sneath (eds.), Microbial classification, Cambridge Univ. Press.

Cunningham, B. and P. Kirk. 1941. The chemical metabolism of Paramecium caudatum. J. Cell. Comp. Physiol. 18: 299-316.

Dewey, V. C., M. R. Heinrich and C. W. Kidder. 1957. Evidence for the absence of the urea cycle in Tetrahymena. J. Protozool. 4: 211-219.

Doyle, W. L. and J. P. Harding. 1937. Quantitative studies on the ciliate Glaucoma. Excretion of ammonia. J. Exp. Biol. 14: 462-469.

Eggert, M. B. 1973. Daily vertical distribution of winter zooplankton in the pelagic zone of Lake Baikal. Hydrobiol. J. 9: 7-14.

Entz, G. Jr. 1909. Studien uber Organisation und Biologie der Tintinniden. Arch. Protistenk. 15: 93-226.

Fenchel, T. 1968. The ecology of marine microbenthos. III. The reproductive potential of ciliates. Ophelia. 5: 137-156.

Gaarder, K. R. 1946. Tintinnoinea. Rep. Sars No. Atl. Deep Sea Exped. 2: 1-37.

Giese, A. C. 1939. Studies on conjugation in Paramecium multimicronucleatum. Am. Nat. 73: 432-444.

Gillbricht, M. 1954. Das Verhalten von Zooplankton-vorzugsweise von Tintinnopsis beroidea Entz--gegenuber thermohalinen-Sprungschichten. Kurz. Mitt. Inst. Fisch. Biol. Univ. Hamb. 5: 32-44.

Gold, K. 1966. The role of ciliates in marine ecology. I. Isolation and cultivation of a member of the order Tintinnida. Am. Zool. 6: 513.

Gold, K. 1968. Some observations on the biology of Tintinnopsis sp. J. Protozool. 15: 193-194.

Gold, K. 1969a. The preservation of tintinnids. J. Protozool. 16: 126-128.

Gold, K. 1969b. Tintinnida: Feeding experiments and lorica development. J. Protozool. 16: 507-509.

Gold, K. 1970. Cultivation of marine ciliates (Tintinnida) and heterotrophic flagellates. Helgol. Wiss. Meeres. 20: 264-271.

Gold, K. 1971. Growth characteristics of the mass-reared tintinnid Tintinnopsis beroidea. Mar. Biol. 8: 105-108.

Gold, K. 1973a. Methods for growing Tintinnida in continuous culture. Am. Zool. 13: 203-208.

Gold, K. 1973b. The effects of food concentration, temperature and salinity on 2 species of Tintinnopsis. J. Protozool. 20: 515.

Gold, K. 1974a. The role of planktonic protozoa in the marine food chain. Seasonal changes, relative abundance and cell size distribution of Tintinnida. AEC Document C00-3390-14.

Gold, K. 1974b. Studies on the size distribution of loricae and the growth status of Tintinnida in Eel Pond. Biol. Bull. 147: 477.

Gold, K. and E. A. Morales. 1974a. Effects of temperature on 2 strains of Tintinnopsis tubulosus. J. Protozool. 21: 442.

Gold, K. and E. A. Morales. 1974b. Size distribution of tintinnids and its importance in ecological studies. J. Protozool. 21: 438.

Gold, K. and E. A. Morales. 1975a. A new hypothesis to account for lorica building by certain Tintinnida. J. Protozool. 22: 38A.

Gold, K. and E. A. Morales. 1975b. Seasonal changes in lorica sizes and the species of Tintinnida in the New York Bight. J. Protozool. 22: 520-528.

Gold, K. and E. A. Morales. 1975c. Tintinnida of the New York Bight: Loricae of Parafavella gigantea, P. parumdentata, and Ptychocylis obtusa. Trans. Amer. Micros. Soc. 94: 142-145.

Gold, K. and E. A. Morales. 1975d. Studies on Woods Hole Tintinnida using scanning electron microscopy. Biol. Bull. 149: 427.

Gold, K. and E. A. Morales. 1976. Observations on the nature and significance of the particles used by Tintinnida during lorica-building. Trans. Amer. Micros. Soc. 95: 69-72.

Goulder, R. 1972. Grazing by the ciliated protozoan Loxodes magnus on the alga Scenedesmus in a eutrophic pond. Oikos. 23: 109-115.

Goulder, R. 1973. Observations over 24 hours on the quantity of algae inside grazing ciliated protozoa. Oecologia. 13: 177-182.

Gran, H. H. 1933. Studies on the biology and chemistry of the Gulf of Maine. II. Distribution of phytoplankton in August, 1932. Biol. Bull. 64: 159-182.

Gran, H. H. and T. Braarud. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). J. Biol. Bd. Canada. 1: 279-467.

Halldal, P. 1953. Phytoplankton investigations from Weather Ship M in the Norwegian Sea 1948-49. Hvalråd. Skr. 38: 1-91.

Hamilton, R. D. and J. E. Preslan. 1969. Cultural characteristics of a pelagic marine hymenostome ciliate, Uronema sp. J. Exp. Mar. Biol. 4: 90-99.

Harding, G. C. H. 1972. Ecological observations on North Atlantic deep-sea copepods. PhD Thesis. Dalhousie Univ. Halifax. 201 p.

Hargrave, B. T. and G. H. Geen. 1968. Phosphorus excretion by zooplankton. Limnol. Oceanogr. 13: 332-342.

Harris, E. 1959. The nitrogen cycle in Long Island Sound. Bull. Bingham Oceanogr. Coll. 17: 31-65.

Hedin, H. 1974. Tintinnids on the Swedish west coast. Zoon. 2: 123-133.

Hensen, V. 1887. Uber die Bestimmung des Plankton oder des im Meere treibenden materials an Pflanzen und Tieren. Ber. dt. wiss. Komn. Meeresforsch. 5: 1-108.

Hofker, J. 1931. Die Bildung der Tintinnengehause. Nederland. Dierk. Veren. Leyden. Tijdschorft. 2: 144-150.

Holmes, R. W. 1956. The annual cycle of phytoplankton in the Labrador Sea 1950-51. Bull. Bingham Ocean. Coll. 16: 1-74.

Ikeda, T. 1974. Nutritional ecology of marine zooplankton. Mem. Fac. Fish. Hokkaido Univ. 22: 1-97.

Johannes, R. E. 1968. Influence of marine protozoa on nutrient regeneration. Limnol. Oceanogr. 10: 434-442.

Kimball, R. F., T. O. Caspersson, G. Svenson and L. Carlson. 1959. Quantitative cytochemical studies on Paramecium aurelia. I. Growth in total dry weight measured by the scanning interference microscope and X-ray adsorption methods. Exp. Cell Res. 17: 160-172.

Kofoid, C. A. and A. S. Campbell. 1929. A conspectus of the marine and fresh-water Ciliata belonging to the suborder Tintinnoinea, with descriptions of new species principally from the Agassiz Expedition to the eastern tropical Pacific, 1904-05. Univ. Calif. Pub. Zool. 34: 1-403.

Kofoid, C. A. and A. S. Campbell. 1939. The Ciliata: the Tintinnoinea. Bull. Mus. Comp. Zool. Harvard. 84: 1-473.

Lackey, J. L. 1936. Occurrence and distribution of the marine protozoan species in the Woods Hole area. Biol. Bull. 70: 264-278.

Laval, M. 1971. Mise en evidence par la microscopie electronique d'un organite d'un type nouveau chez les cilies Tintinnides. C. R. Acad. Sci. 273: 1383-1386.

Laval, M. 1972. Ultrastructure de Petalotricha ampulla (Fol). Comparison avec d'autres Tintinnides et avec les autres ordres de cilies. Protistologica. 8: 369-386.

Laval, M. 1973. Cortex et perilemme de Cyttarocylis brandti (cilie Tintinnide). Remarques sur les structures corticales des cilies. J. Cell Biol. 59: 246.

Ling, H. 1965. The tintinnid Parafavella gigantea (Brandt), Kofoid & Campbell, 1929, in the North Pacific Ocean. J. Paleont. 39: 721-723.

Loeblich, A. R., Jr. and H. Tappan. 1968. Annotated index to genera, subgenera and suprageneric taxa of the ciliate order Tintinnida. J. Protozool. 15: 185-192.

Lohmann, H. 1908. Untersuchungen zur Festellung des vollstandigen Gehaltes des Meeres an Plankton. Wiss. Meeresunters. (Abt. Kiel). 10: 129-370.

Lwoff, A. and N. Roakheiman. 1926. Variations de quelques formes d'azote dans une culture pure d'infusoires. C. R. Acad. Sci, Paris. 183: 156-158.

McCarthy, J. J. 1970. A urease method for urea in seawater. Limnol. Oceanogr. 15 309-313.

Margalef, R. 1963. Role des cilies dans le cycle de la vie pelagique en Mediterranee. Rapp. Proc. Verb. Reun. Comm. Int. Expl. M. Medit. 17: 511-512.

Marshall, S. M. 1969. Protozoa--Order: Tintinnida. Fiches d'identification du zooplankton. Cons. Perm. Int. Expl. Mer. Sheets 117-127.

Mulford, R. A. 1972. An annual plankton cycle on the Chesapeake Bay in the vicinity of Calvert Cliffs, Maryland. Proc. Acad. Nat. Sci., Phila. 124: 17-40.

Needler, B. 1949. Paralytic shellfish poisoning and Gonyaulax tamarensis. J. Fish. Res. Bd. Canada. 7: 490-504.

Nardone, R. M. and C. G. Wilber. 1950. Nitrogenous excretion in Colpidium campylum. Proc. Soc. Exp. Biol. N. Y. 75: 559-561.

Nutt, D. C. 1963. Fjords and marine basins of Labrador. Polar Notes. 5: 9-24.

Pavlovskaya, T. V. 1973. Influence of feeding conditions on the rate of food consumption and the time of generation in ciliates. Zool. Zhurn. 52: 1451-1457.

Pielou, C. 1974. Population and community ecology: principles and methods. Gordon and Breach. New York. 424p.

Posta, A. 1963. Etude des Tintinnides de Villefranche. Cahiers. de Biol. Mar. 4: 201-210.

Prakash, A. 1963. Source of paralytic shellfish tox[illegible] the Bay of Fundy. J. Fish. Res. Ed. Canada. 20: 983-996.

Rapport, D. J., J. Berger and D. B. W. Reid. 1972. Determination of food preference of Stentor coeruleus. Biol. Bull. 142: 103-109.

Seaman, G. R. 1954. Enzyme systems in Tetrahymena pyriformis S. VI. Urea formation and breakdown. J. Protozool. 1: 207-210.

Silva, E. S. 1950. Les nintinnides de la Baie de Cascais (Portugal). Bull. Inst. Ocean. Monaco. 979: 1-28.

Smith, S. L. 1975. The role of zooplankton in the nitrogen dynamics of marine systems. PhD Thesis. Duke Univ. North Carolina.

Soldo, A. T. and W. J. van Wagtendonk. 1961. Nitrogen metabolism in Paramecium aurelia. J. protozool. 8: 41-55.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799-801.

Sonneborn, R. M. 1939. Sexuality and related problems in Paramecium. Coll. Net. 14: 77-84.

Spittler, P. 1973. Feeding experiments with tintinnids. Oikos Supp. 15: 128-132.

Stein, J. R. 1975. Handbook of phycological methods. Culture methods and growth measurements. Cambridge Univ. Press. 448p.

Summers, L. G. 1963. Variation of cell and nuclear volume of Tetrahymena pyriformis with three parameters of growth: age of culture, age of cell, and generation time. J. Protozool. 10: 288-293.

Utermohl, H. 1931. Neue wege in der quantitativen Erfassung des Planktons. Eerh. Int. Limnol. 5: 567-596.

Vitiello, P. 1964. Contribution a l'etude des Tintinnides de la baie d'Alger. Pelagos. 2: 5-42.

Wailes, G. H. 1924. Tintinnidae from the Strait of Georgia, B. C. Cont. Can. Biol. 2: 533-543.

Weatherby, J. H. 1929. Excretion of nitrogenous substances in protozoa. Physiol. Zool. 2: 375-394.

Webb, T. L. and D. Francis. 1969. Mating types in Stentor coeruleus. J. Protozool. 16: 758-763.

Wright, R. 1907. The plankton of eastern Nova Scotia waters. Cont. Can. Biol. 1901-1907. Ses. Paper 22A. 19p.

Yentsch, C. S. and J. H. Ryther. 1958. Relative significance of the net phytoplankton and nanoplankton in the waters of Vineyard Sound. J. du Conseil. 24: 231-238.

Zaika, V. Ye. and N. A. Ostrovskaya. 1972. Pattern of diurnal variations in microzooplankton abundance in the surface layer of the Mediterranean Sea. Oceanology. 12: 725-729.

Zeizschel, B. 1966. Die Verbreitung der Tintinnen im Nordatlantik. Veroffent. Inst. Meersforsch. Bremerhaven. 2: 292-300.

Zeizschel, B. 1967. Bedeutung der Tintinnen als Glied der Nahrungskette. Helgoland. Wiss. Meeresunters. 15: 589-601.

Zeitzschel, B. 1969. Tintinnen des westlichen Arabischen Meeres, ihre Bedeutung als Indikatoren fur Wasserkorper und Flied der Nahrungskette. "Meteor" Forschungs. Herausgegeben von der Deutsch. Forschungs. Reihe D. 4: 47-101.

APPENDIX A

Figure 1.

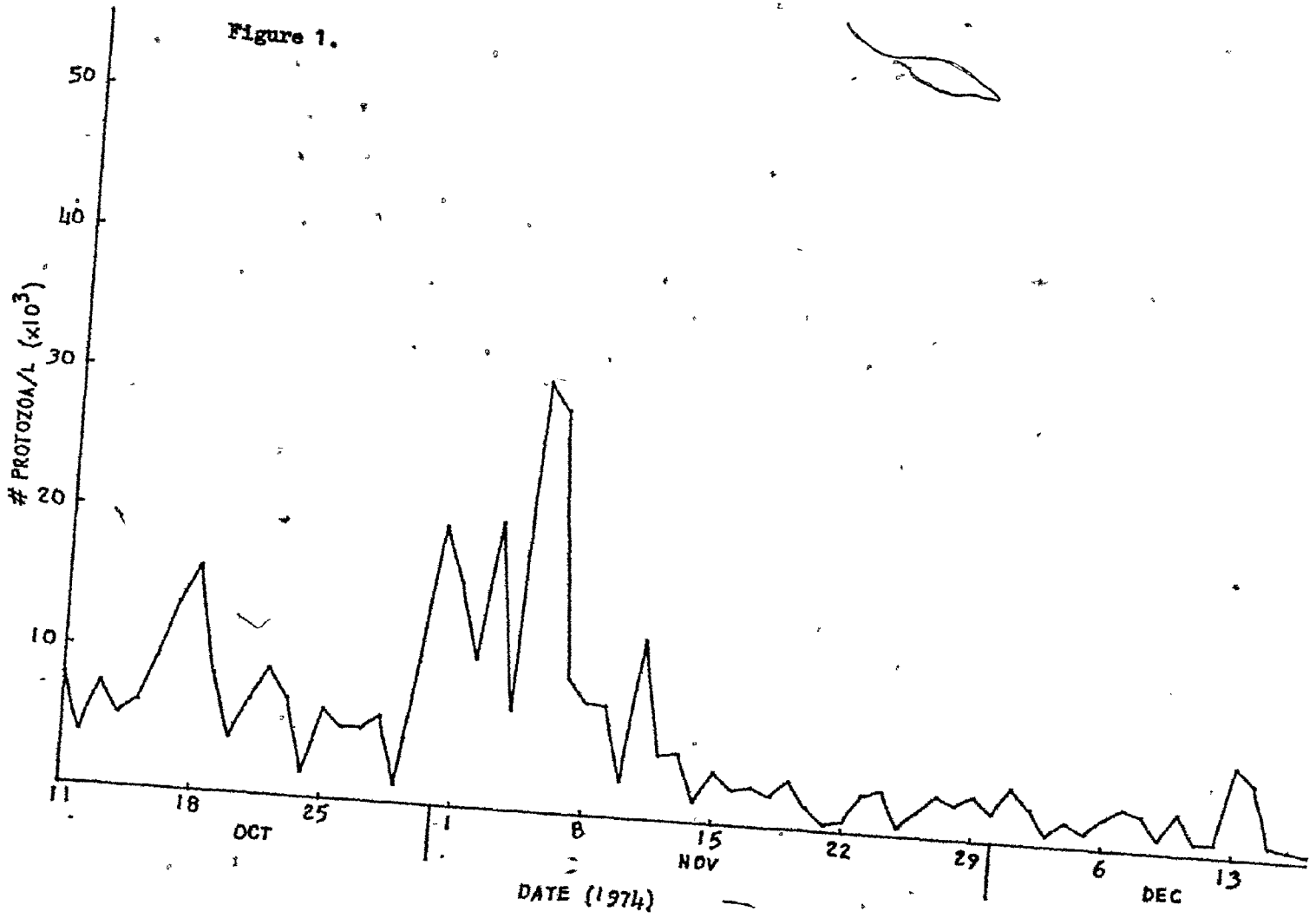
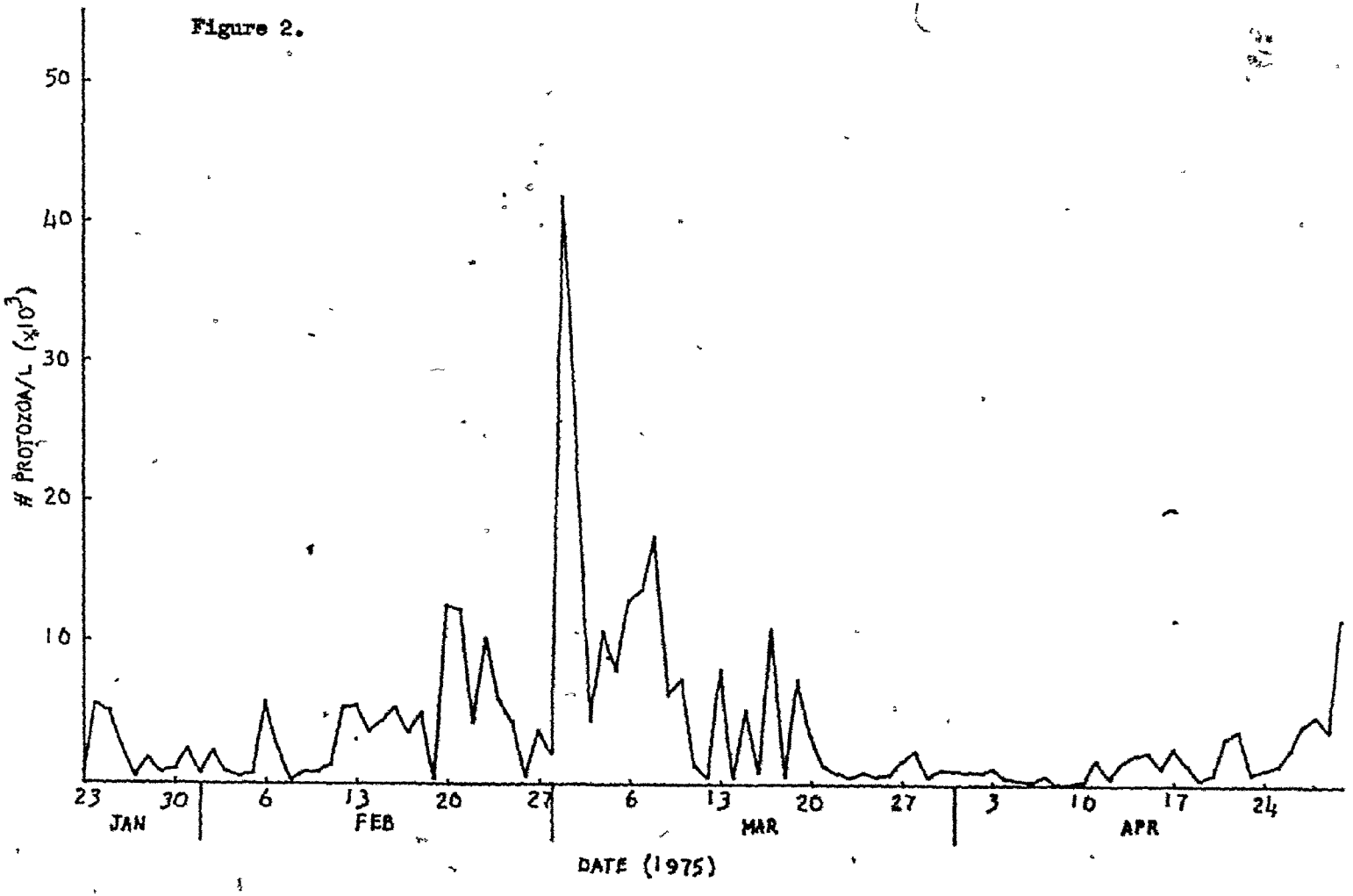

PROTOZOA/L (x10^3)
50
40
30
20
10
11
18
25
OCT
1
8
15
NOV
22
29
6
13
DEC
DATE (1974)

Figure 2.


PROTOZOA/L (x10^3)
50
40
30
20
10
23
30
6
13
20
27
6
13
20
27
3
10
17
24
JAN
FEB
MAR
APR
DATE (1975)

A2

Figure 3.

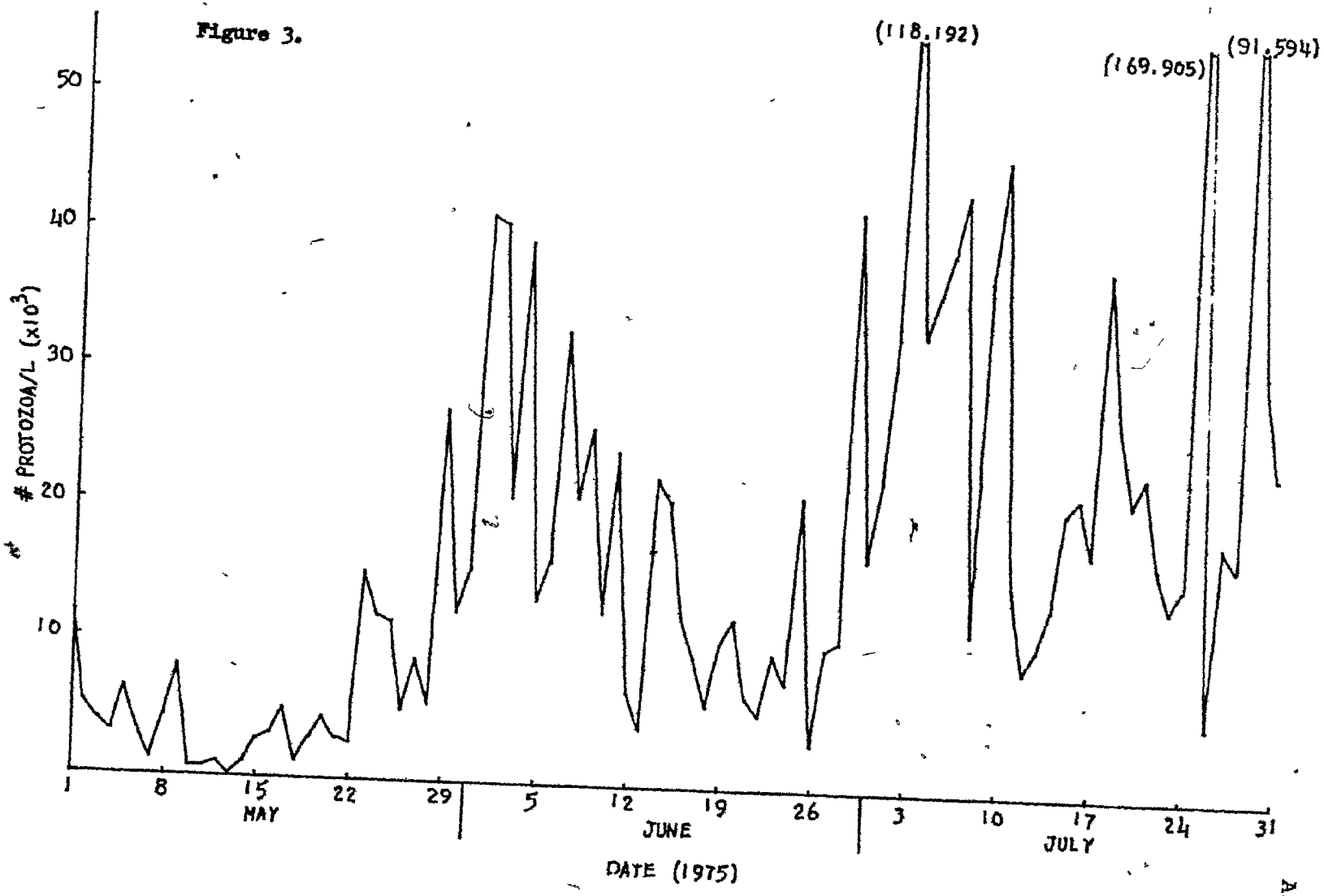

(118,192)
(169,905)
(91,594)
50
40
30
20
10
PROTOZOA/L (x10³)
1
8
15
22
29
5
12
19
26
3
10
17
24
31
MAY
JUNE
JULY
DATE (1975)

Figure 4.

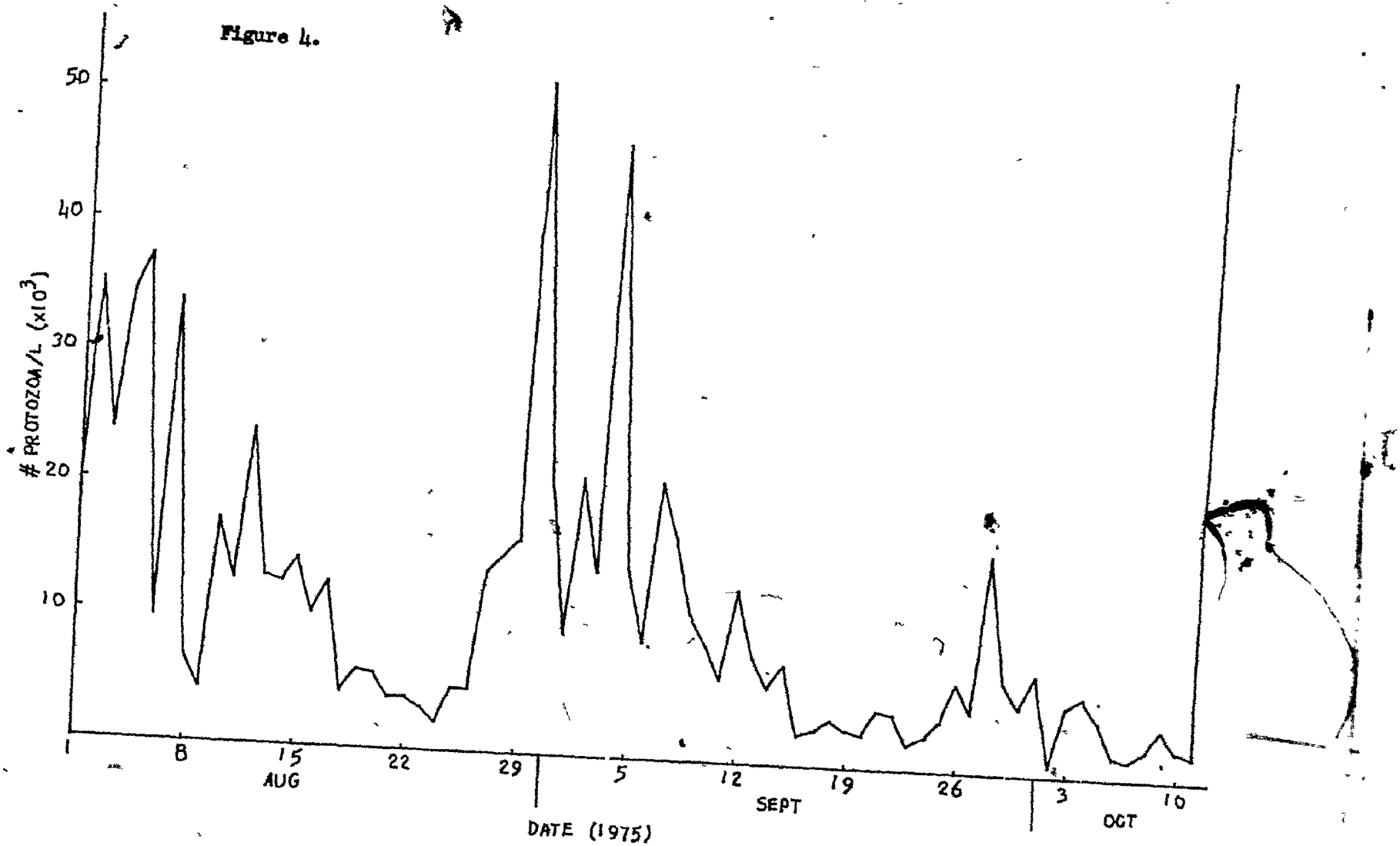

50
40
30
20
10
PROTOZOA/L (x10³)
1
8
15
22
29
5
12
19
26
3
10
AUG
SEPT
OCT
DATE (1975)

Figure 5.

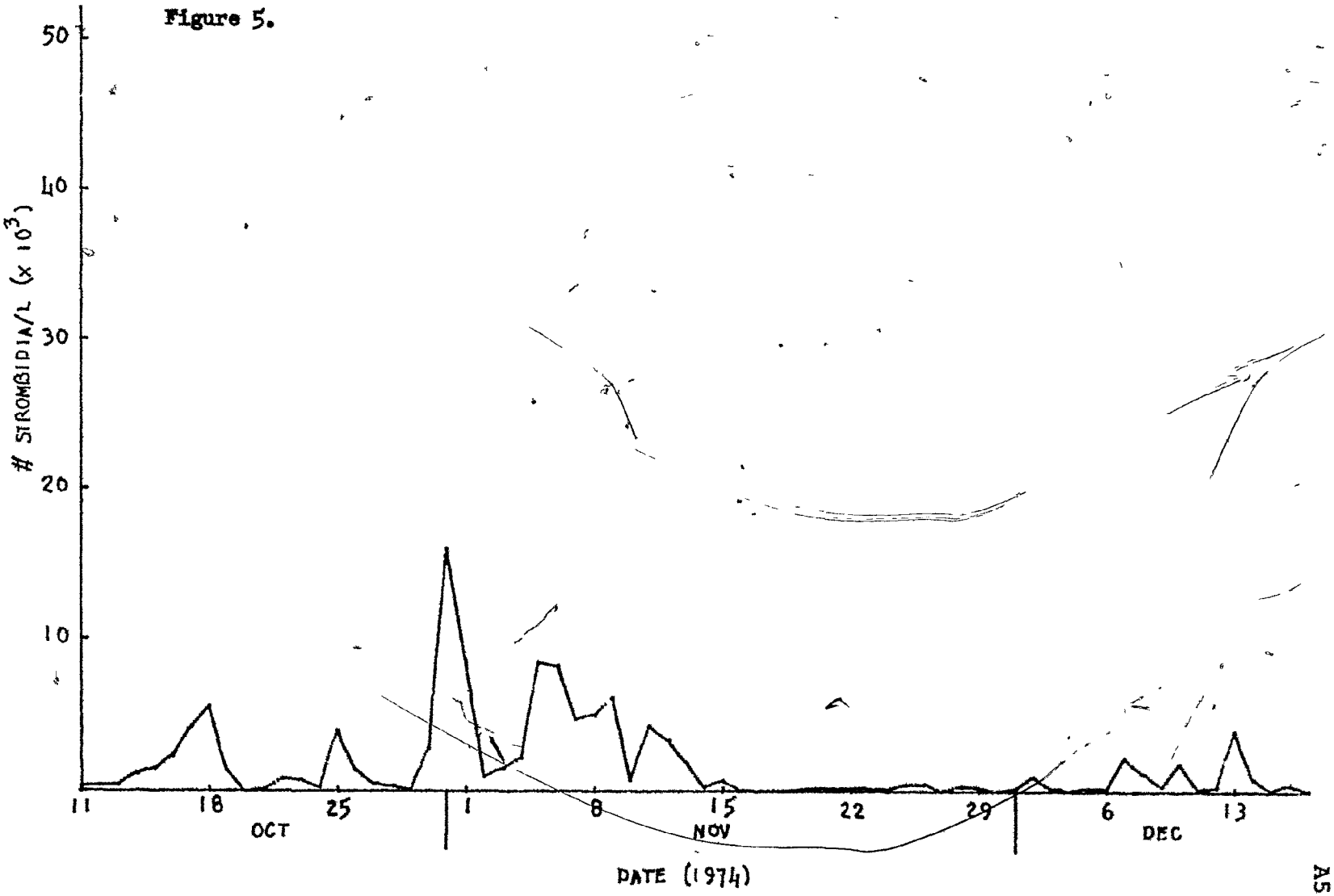

STROMBIDIA/L (x 10^3)
50
40
30
20
10
11
18
25
1
8
15
22
29
6
13
OCT
NOV
DEC
DATE (1974)

Figure 6.

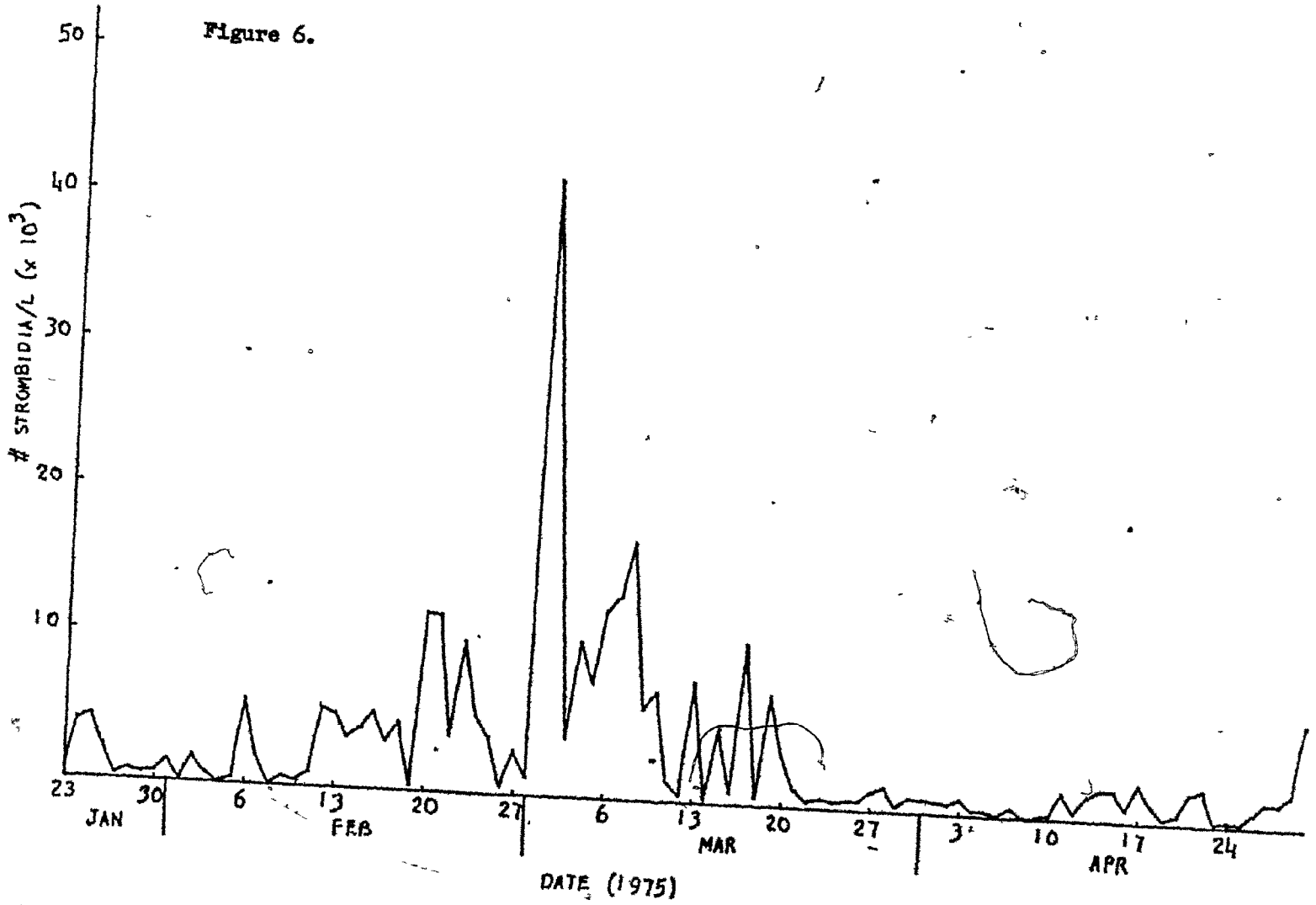

STROMBIDIA/L (x 10³)
50
40
30
20
10
23
30
6
13
20
27
6
13
20
27
3
10
17
24
JAN
FEB
MAR
APR
DATE (1975)

Figure 7.

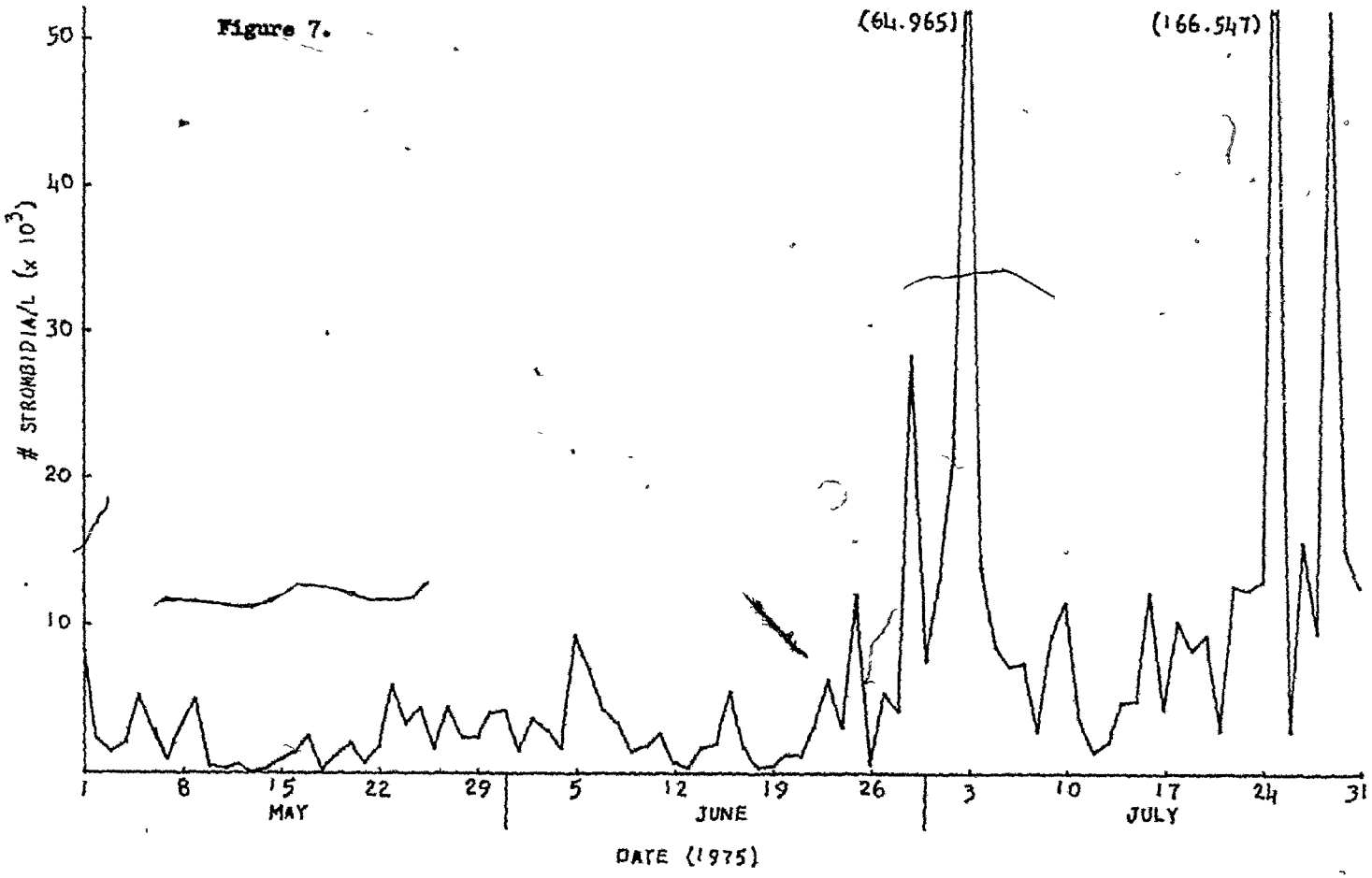

(64.965)
(166.547)
50
40
30
20
10
STROMBIDIA/L (x 10^3)
1
8
15
22
29
5
12
19
26
3
10
17
24
31
MAY
JUNE
JULY
DATE (1975)

Figure 8.

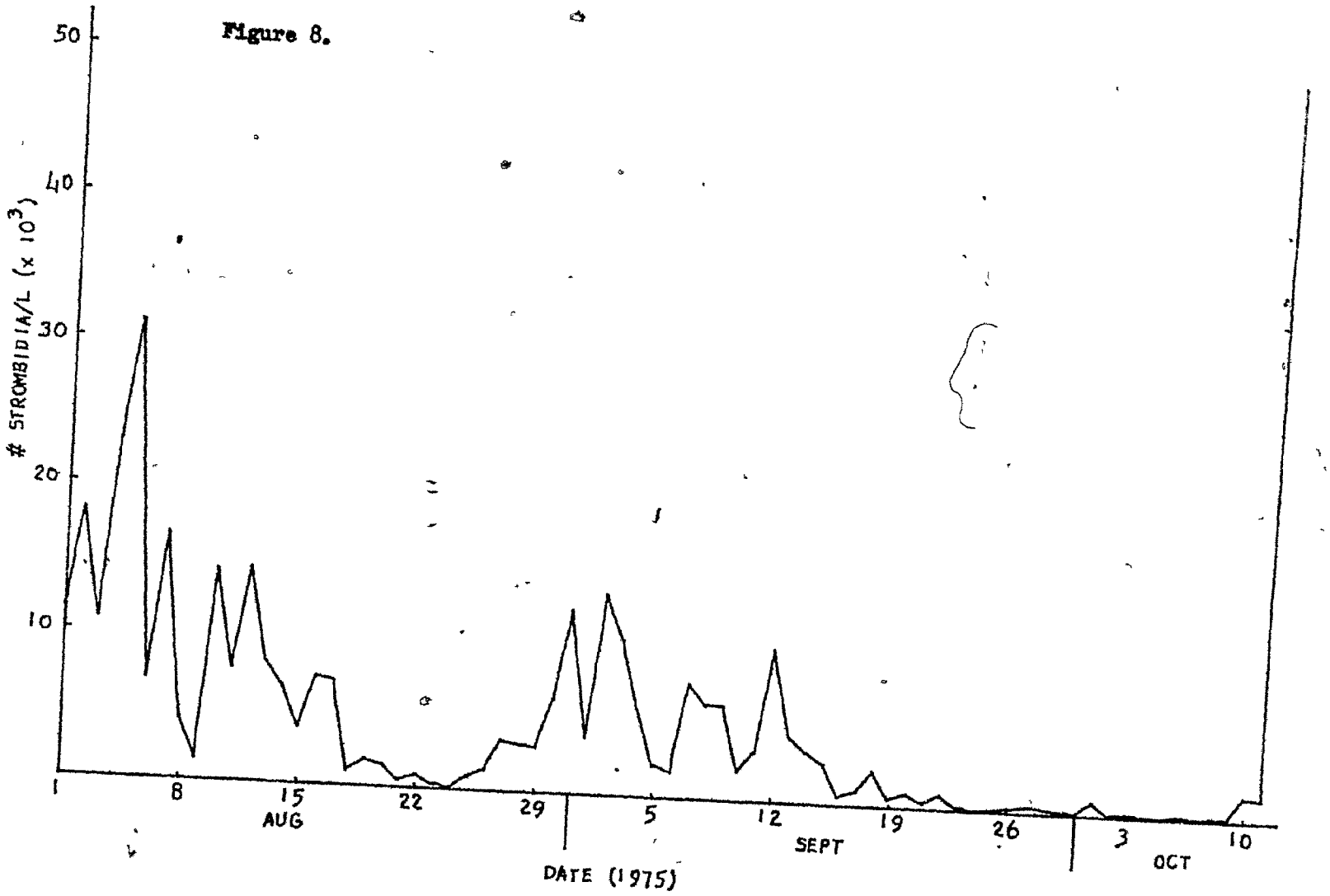

STROMBIDIA/L (x 10^3)
50
40
30
20
10
1
8
15
22
29
5
12
19
26
3
10
AUG
SEPT
OCT
DATE (1975)

Figure 9.

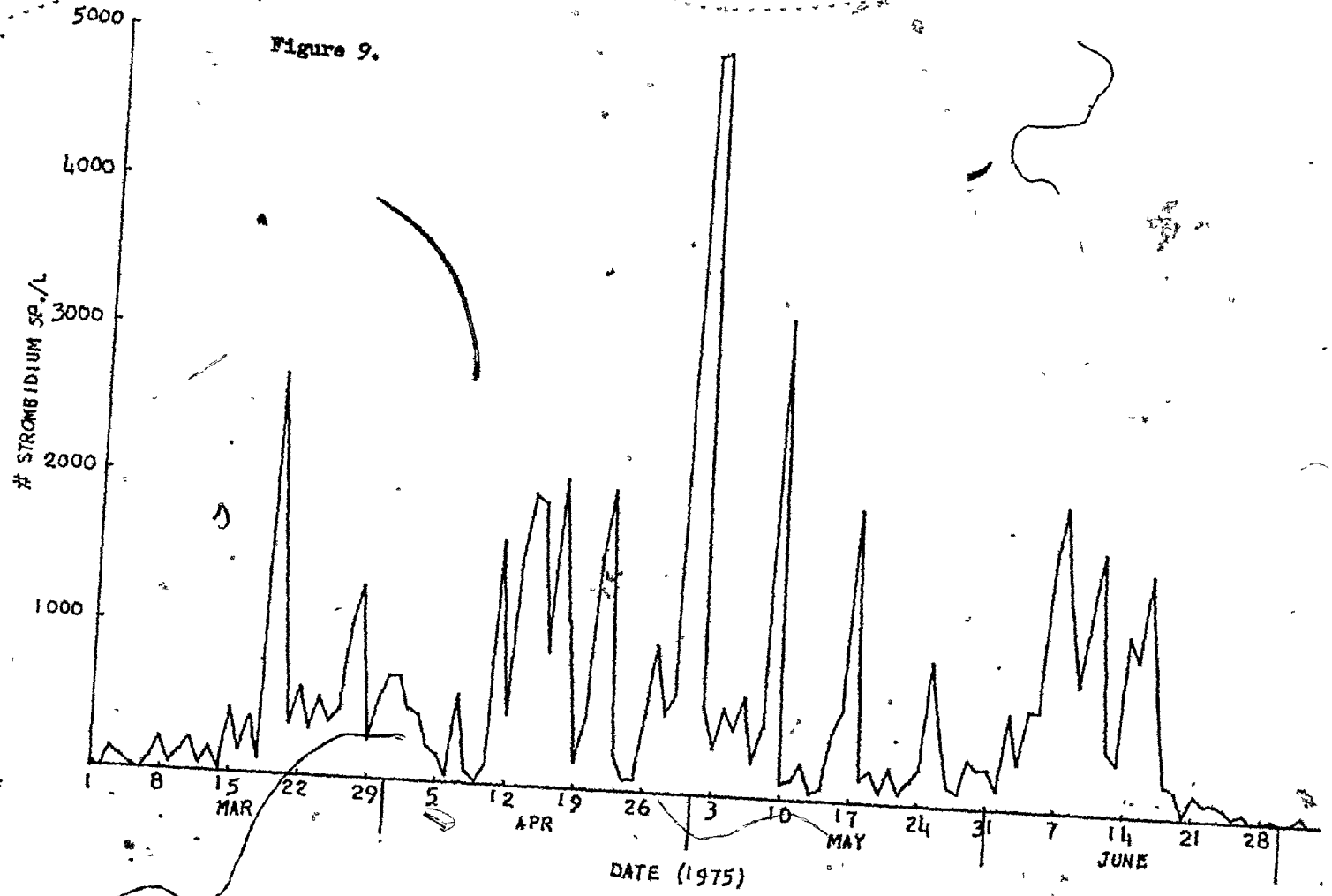

5000
4000
3000
2000
1000
STROMBIDIUM SP./L
1
8
15
22
29
5
12
19
26
3
10
17
24
31
7
14
21
28
MAR
APR
MAY
JUNE
DATE (1975)

Figure 10.

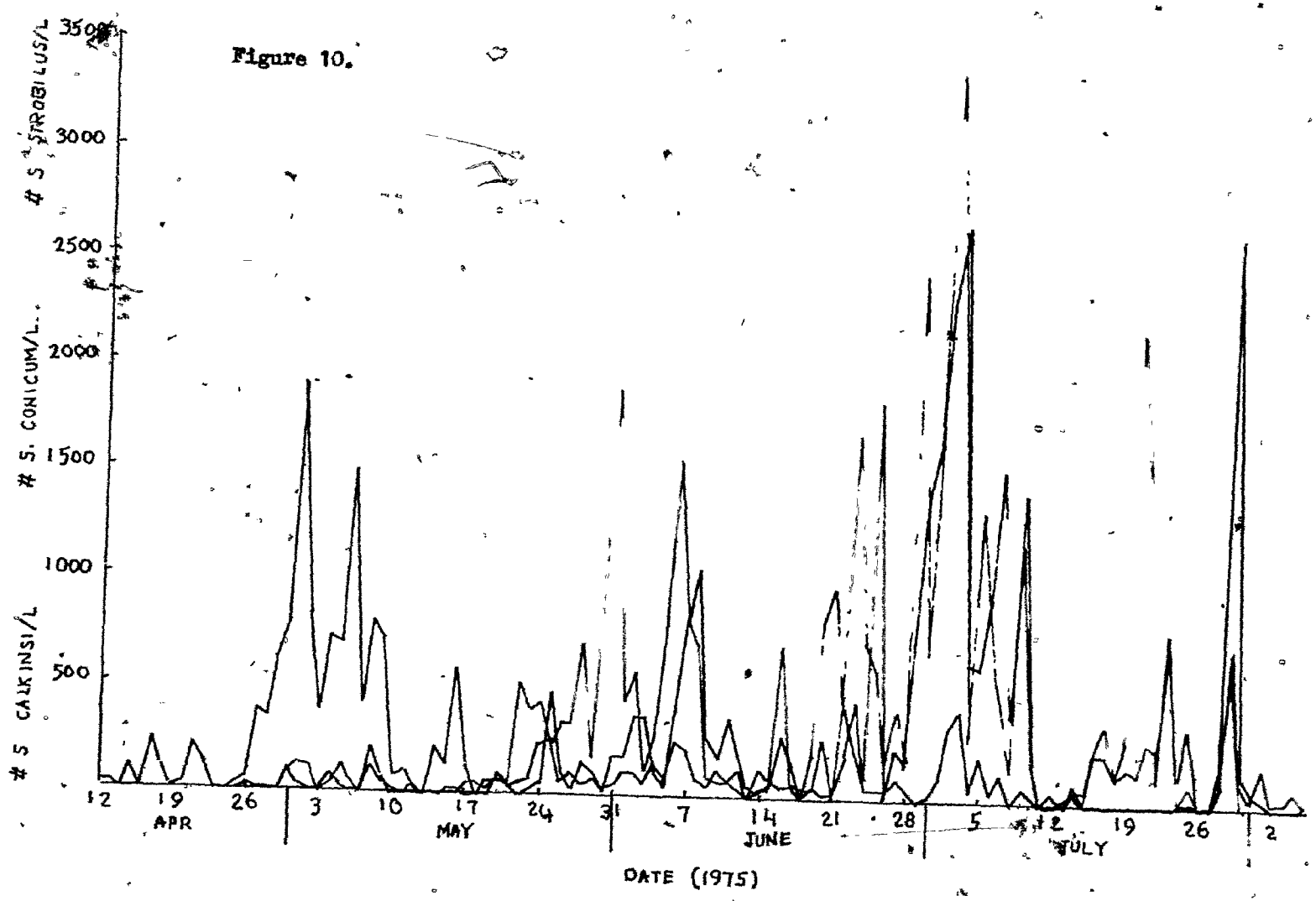

S. STROBILUS/L
S. CONICUM/L
S. CALKINSI/L
3500
3000
2500
2000
1500
1000
500
12
19
26
APR
3
10
17
24
31
MAY
7
14
21
28
JUNE
5
12
19
26
JULY
2
DATE (1975)

Figure 11.

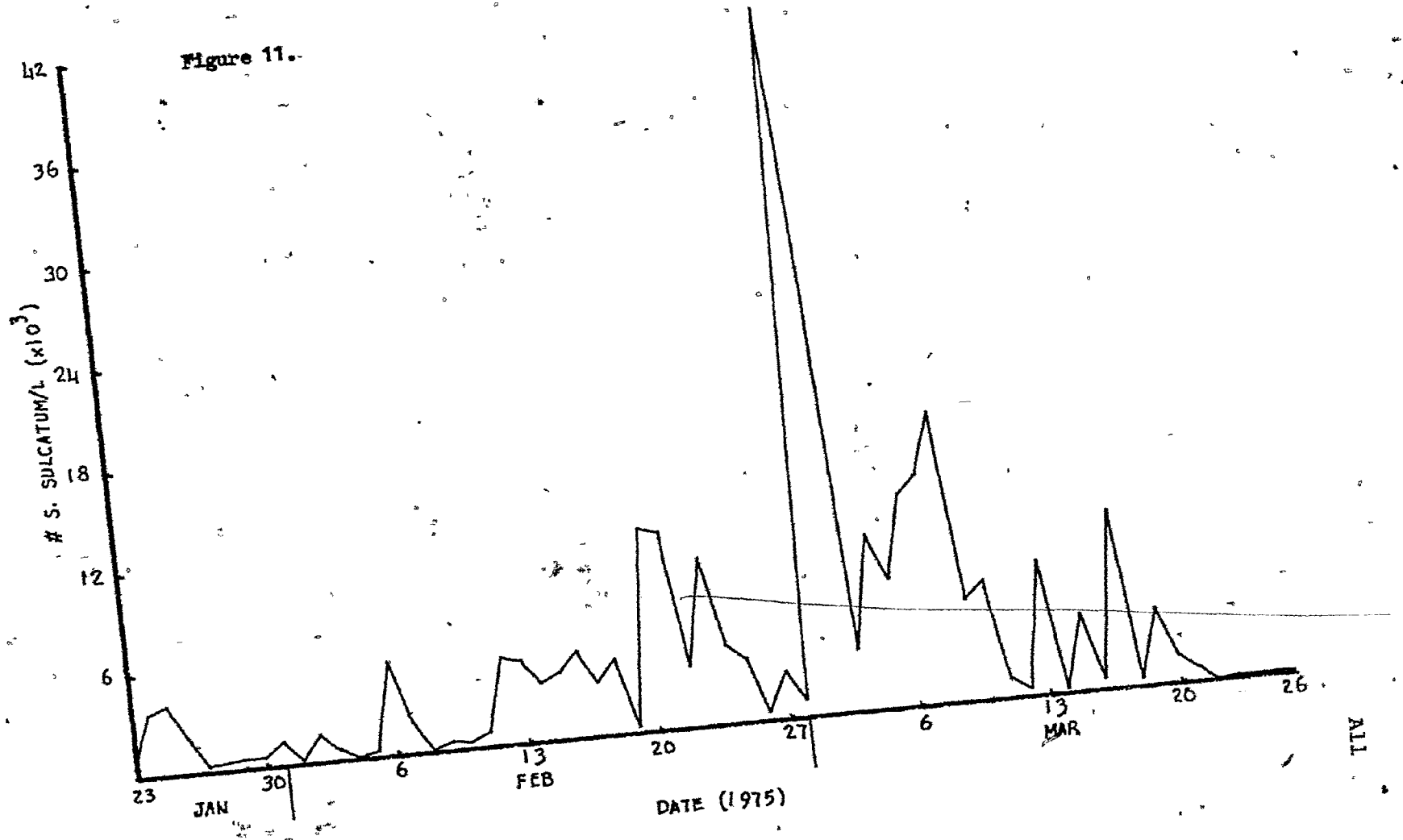

S. SULCATUM/L (x10^3)
42
36
30
24
18
12
6
23
JAN
30
6
13
FEB
20
27
6
13
MAR
20
26
DATE (1975)
All

Figure 12.

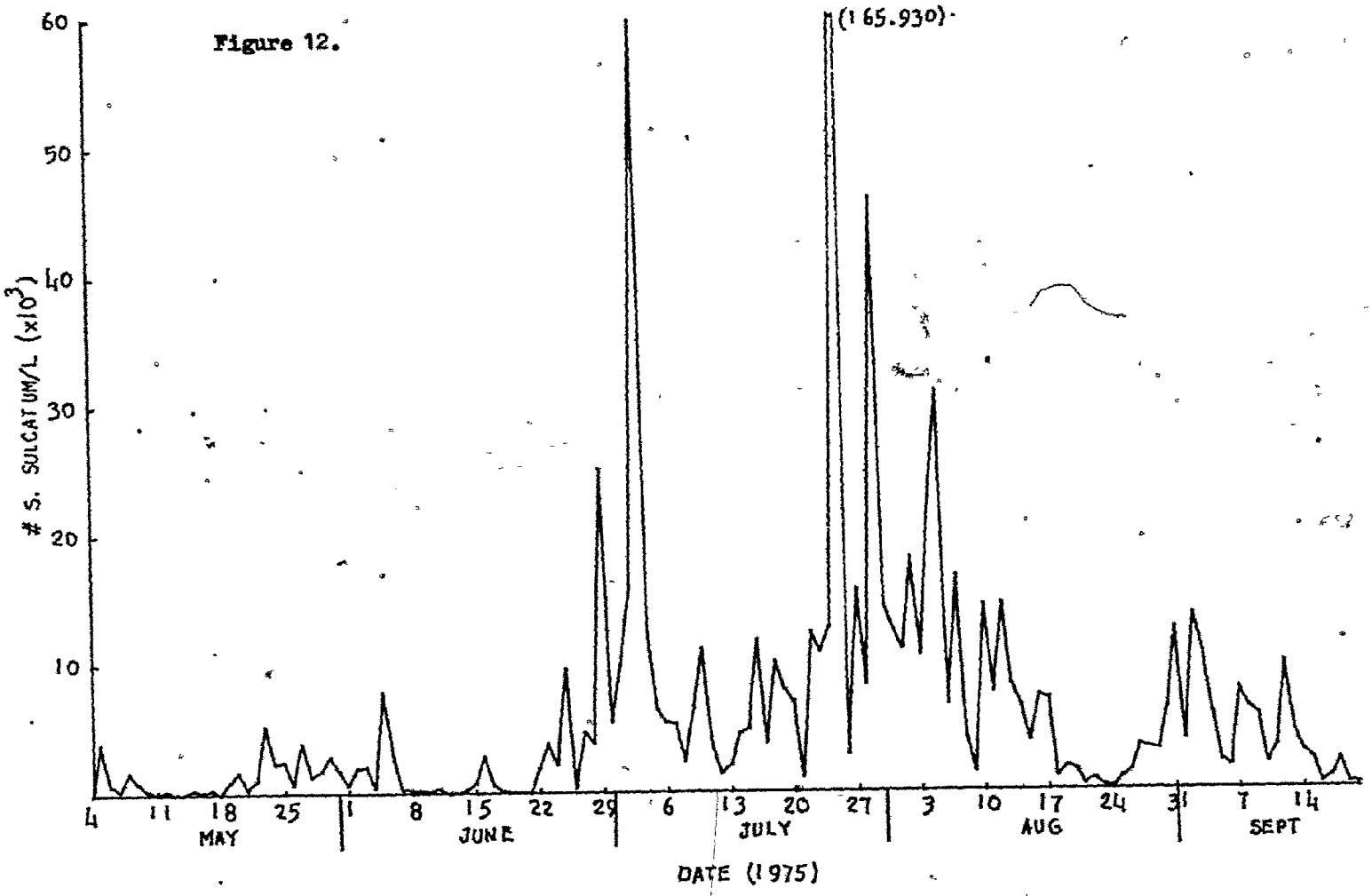

(165.930)
60
50
40
30
20
10
S. SULCATUM/L (x10³)
4
11
18
25
1
8
15
22
29
6
13
20
27
3
10
17
24
31
7
14
MAY
JUNE
JULY
AUG
SEPT
DATE (1975)

Figure 13.

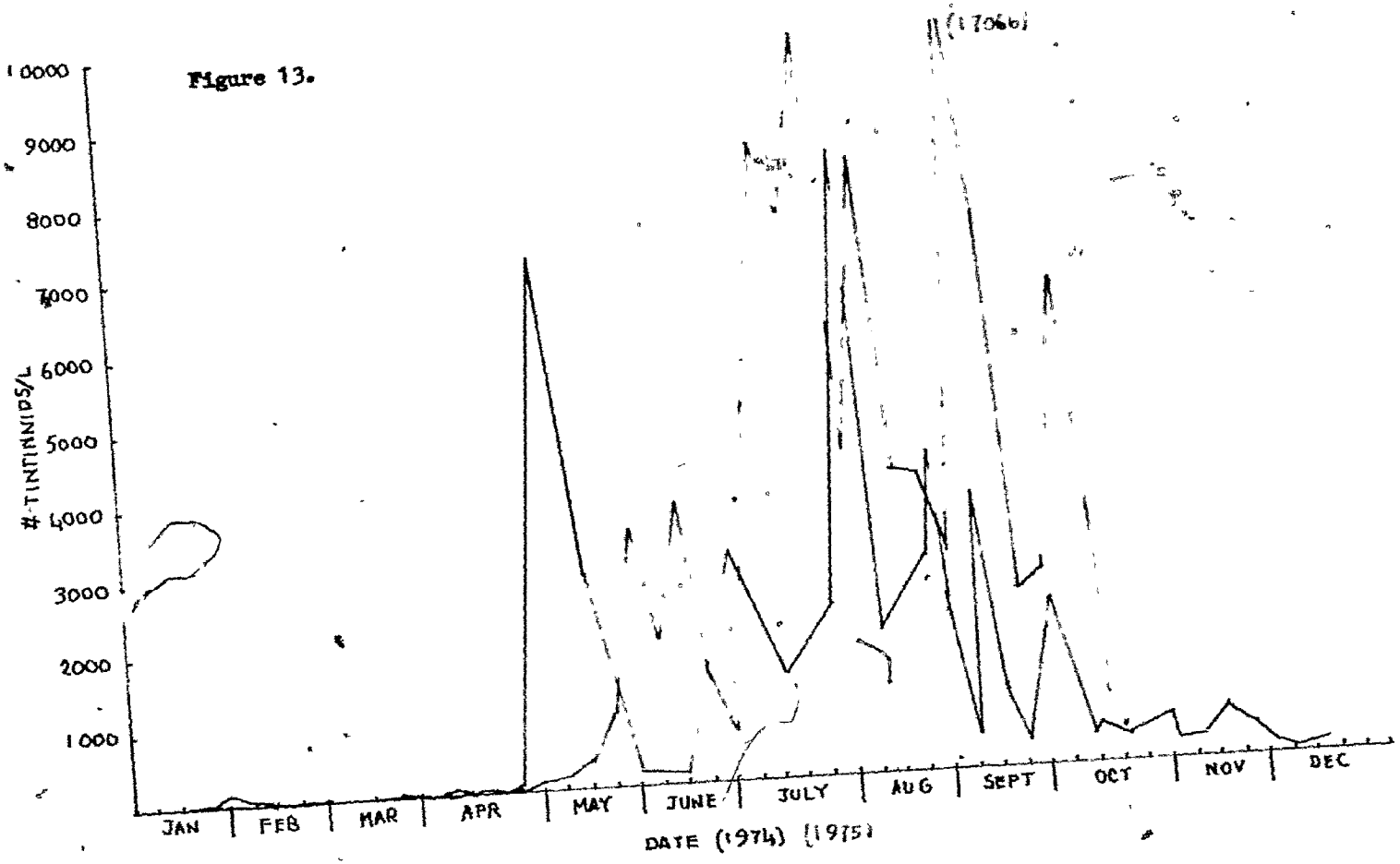

(17066)
10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
#-TINTINNIDS/L
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1974) (1975)

Figure 14.

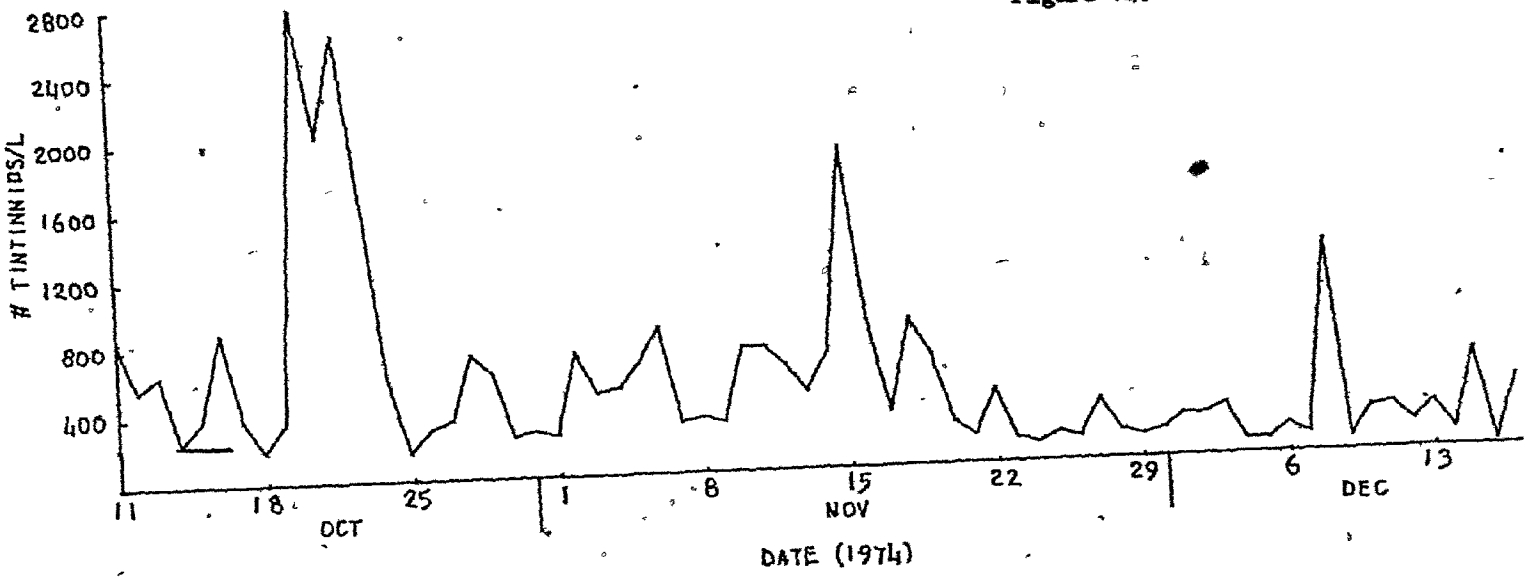
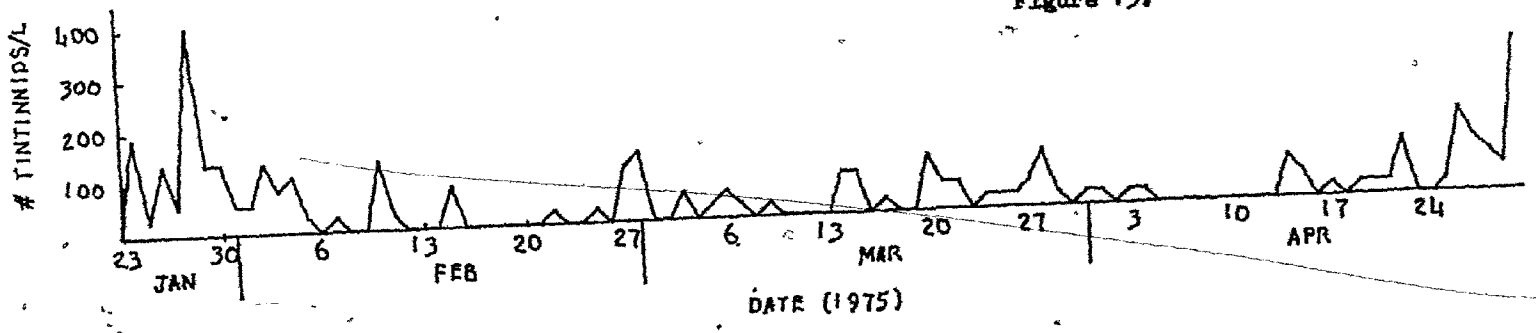


Figure 15.



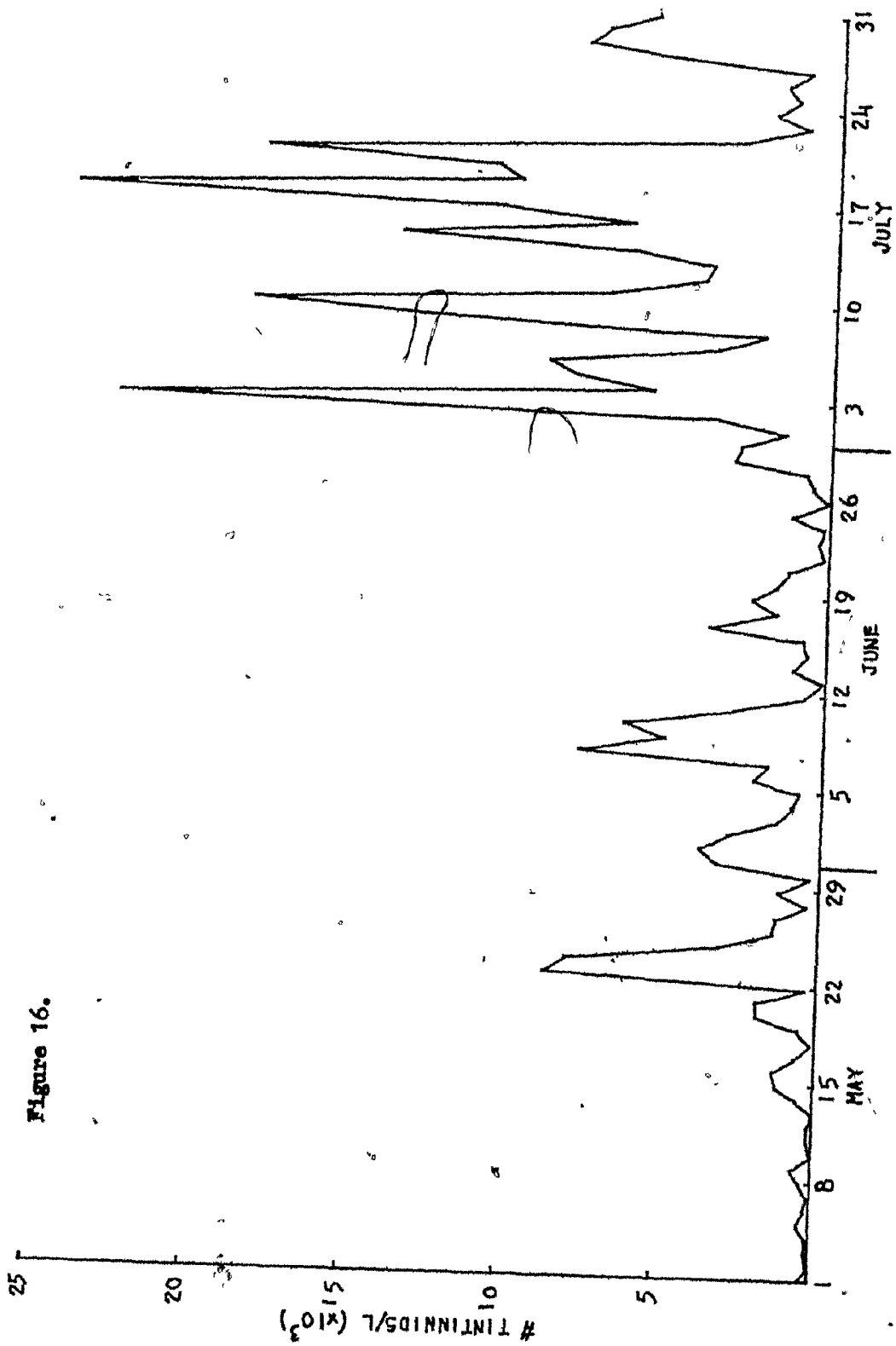

TINTINNIDS/L (x10³)
25
20
15
10
5
1
8
15
22
29
5
12
19
26
3
10
17
24
31
MAY
JUNE
JULY
DATE (1975)

Figure 16.

Figure 17.

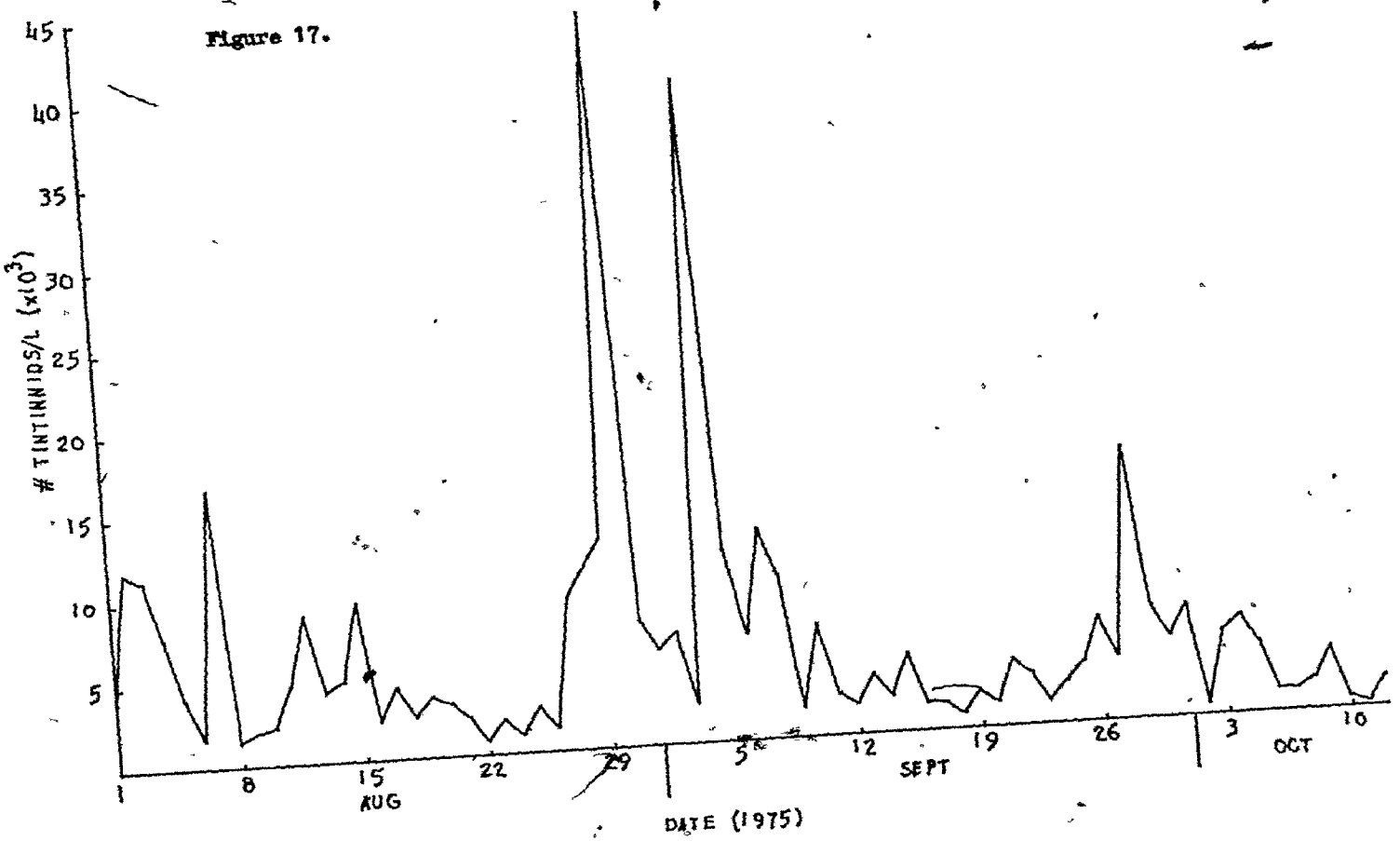

TINTINNIDS/L (x10^3)
45
40
35
30
25
20
15
10
5
1
8
15
22
29
5
12
19
26
3
10
AUG
SEPT
OCT
DATE (1975)

Figure 18.

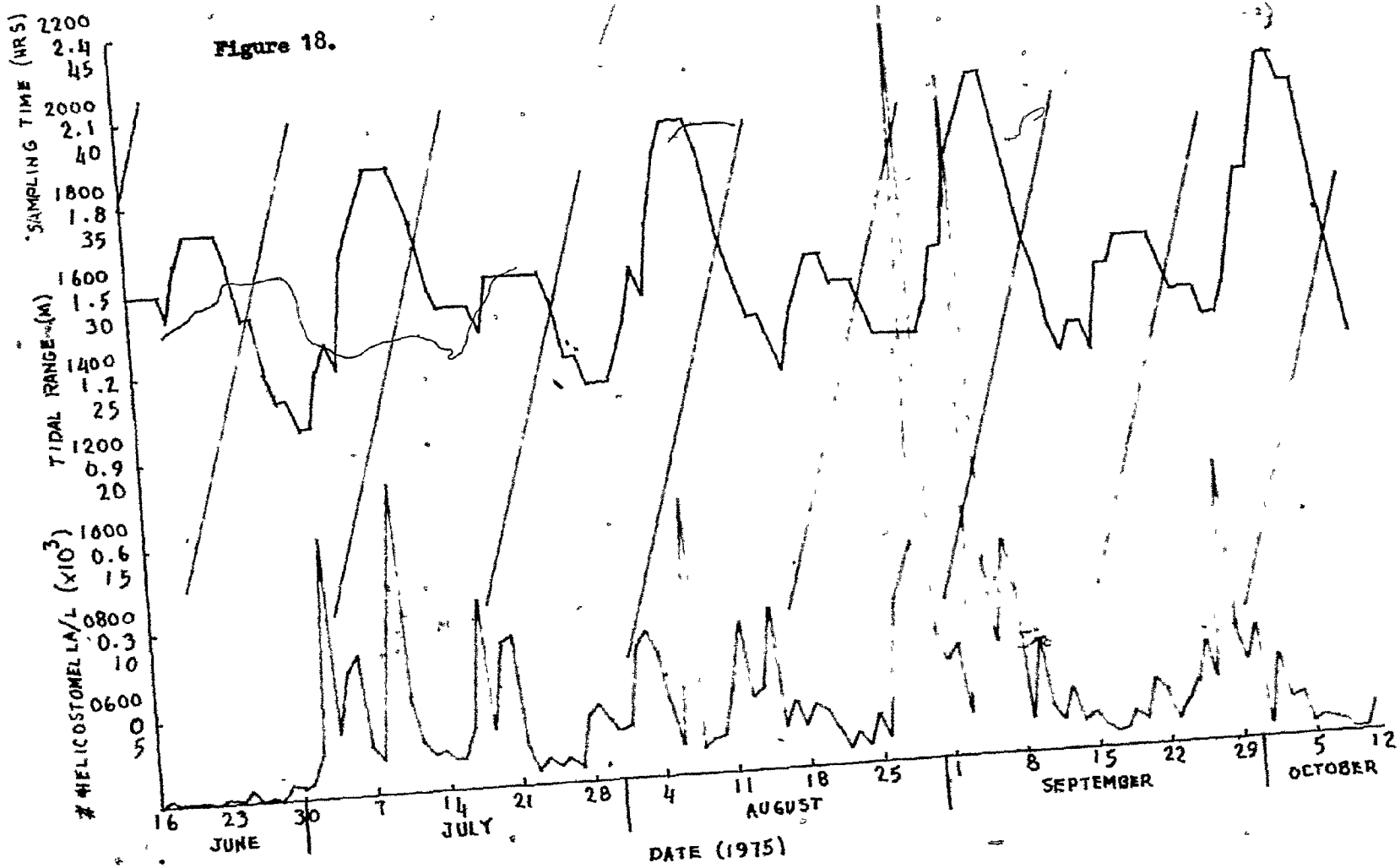
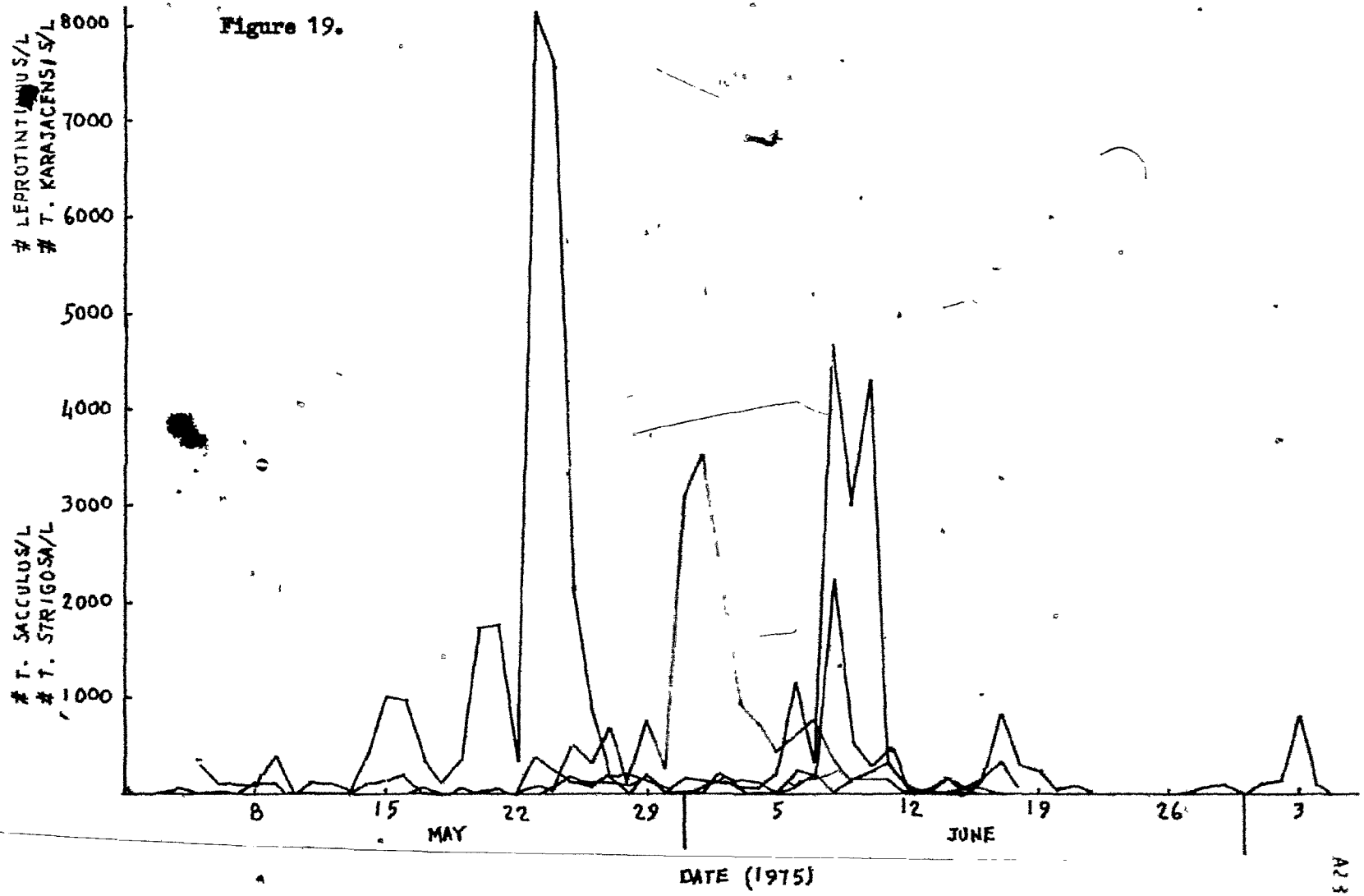

SAMPLING TIME (HRS)
TIDAL RANGE-(M)
#HELICOSTOMELLA/L (X10³)
2200
2000
1800
1600
1400
1200
1600
0800
0600
2.4
2.1
1.8
1.5
1.2
0.9
0.6
0.3
0
45
40
35
30
25
20
15
10
5
16
23
30
7
14
21
28
4
11
18
25
1
8
15
22
29
5
12
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
DATE (1975)

Figure 19.



A13

A18

Figure 20.

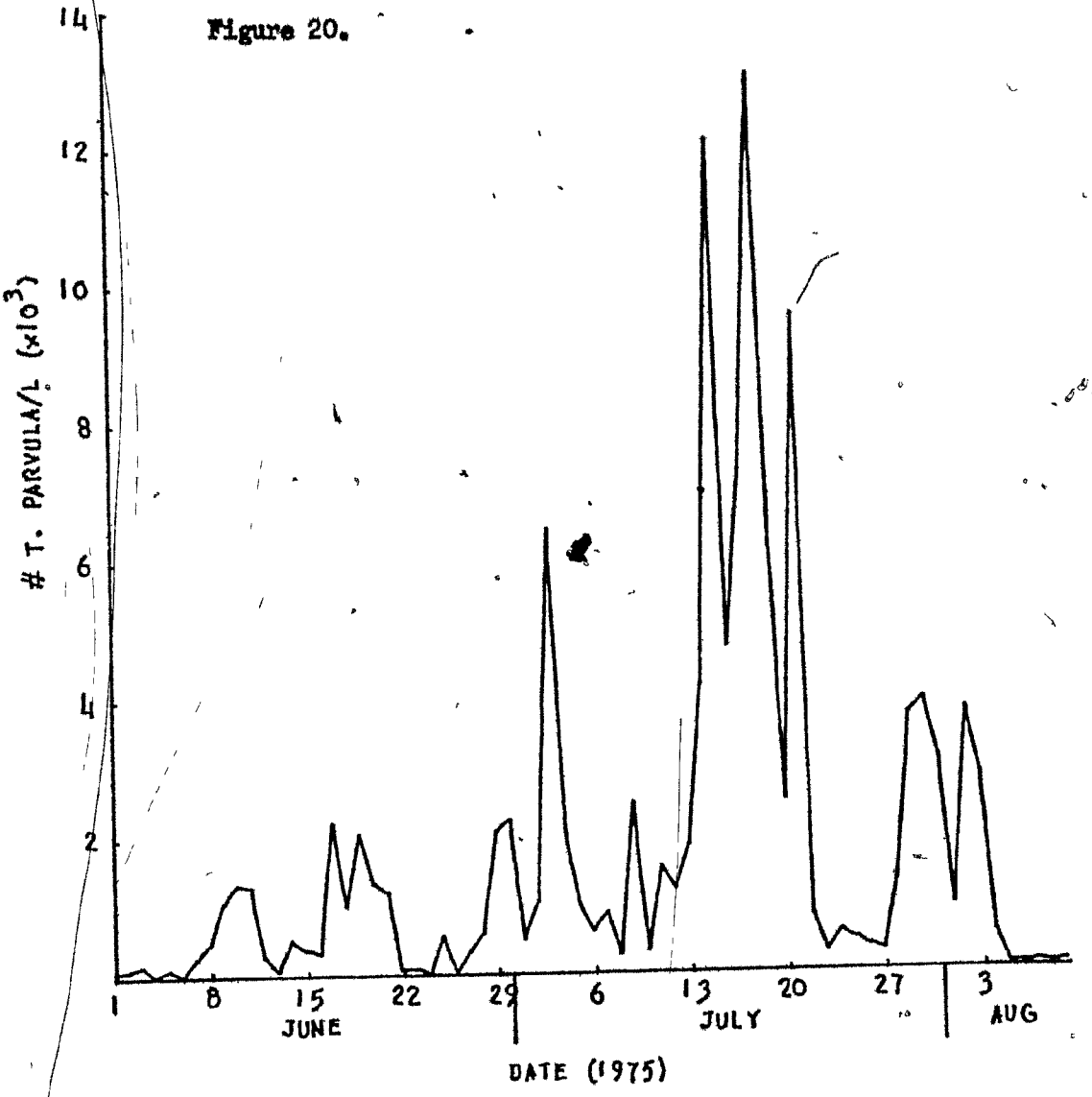
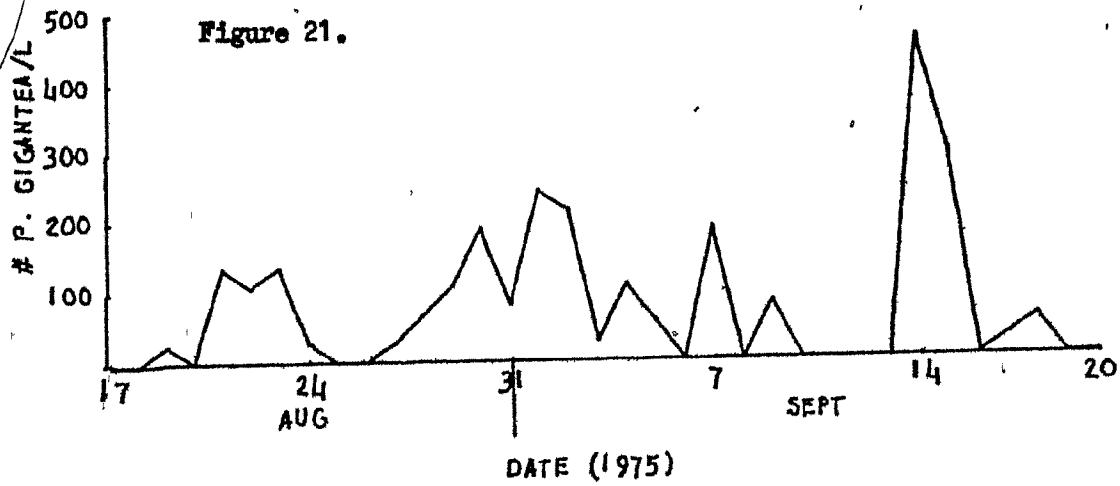


Figure 21.



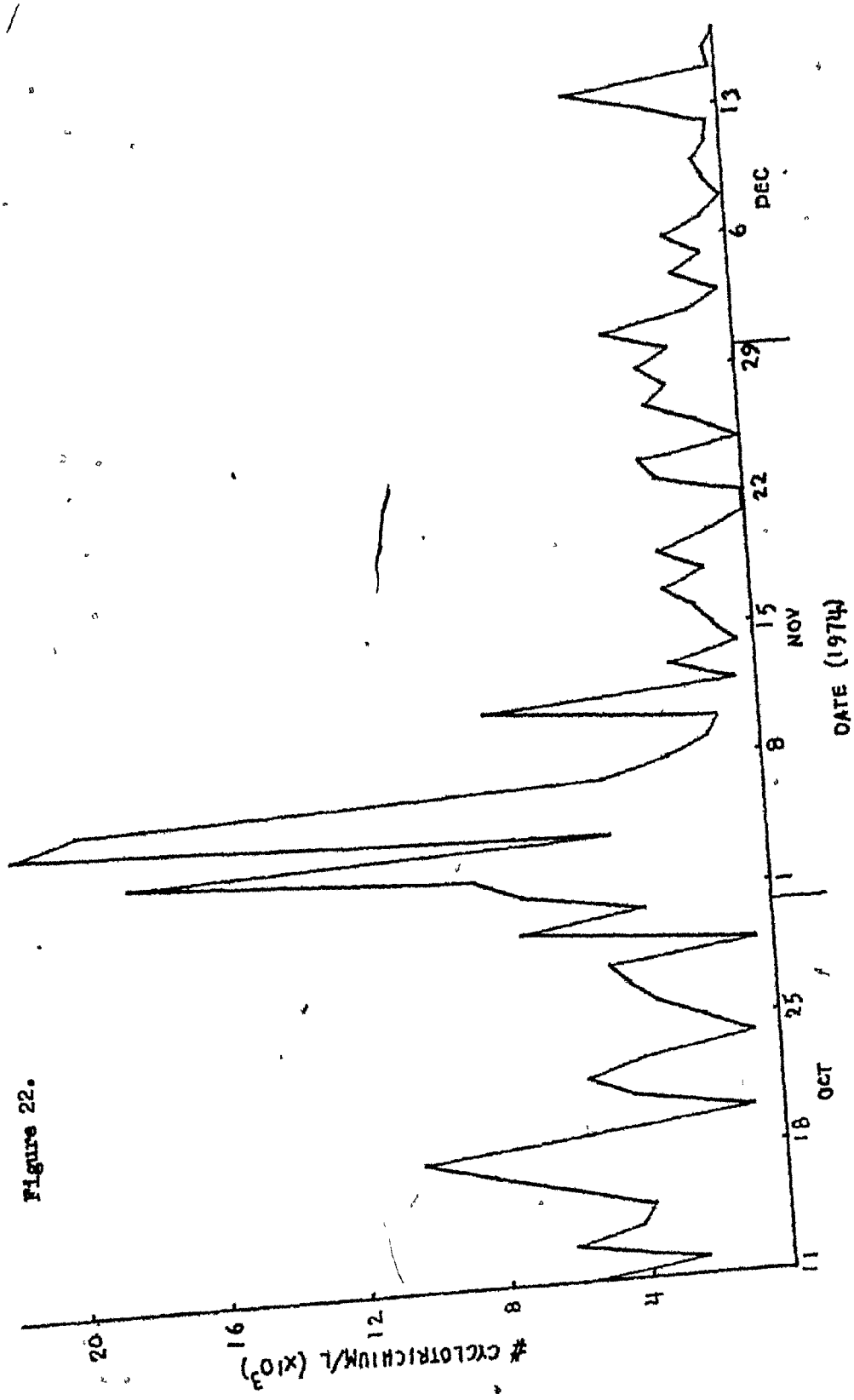

CYCLOTRICHIUM/L (x10³)
4
8
12
16
20
11
18
25
1
8
15
22
29
6
13
OCT
NOV
DEC
DATE (1974)

Figure 22.

Figure 23.

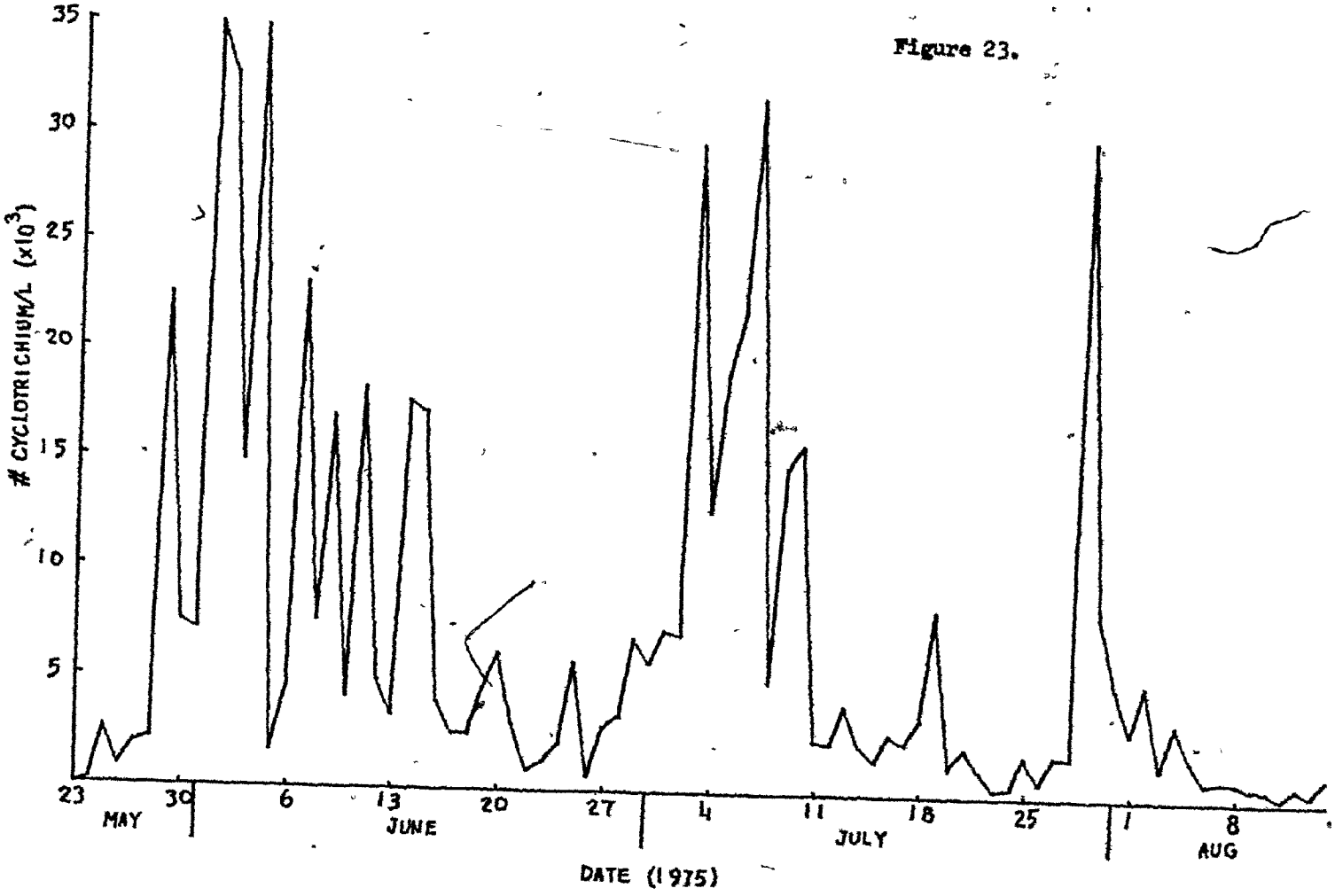

CYCLOTRICHIUM/L (x10^3)
35
30
25
20
15
10
5
23
30
6
13
20
27
4
11
18
25
1
8
MAY
JUNE
JULY
AUG
DATE (1975)

Figure 24.

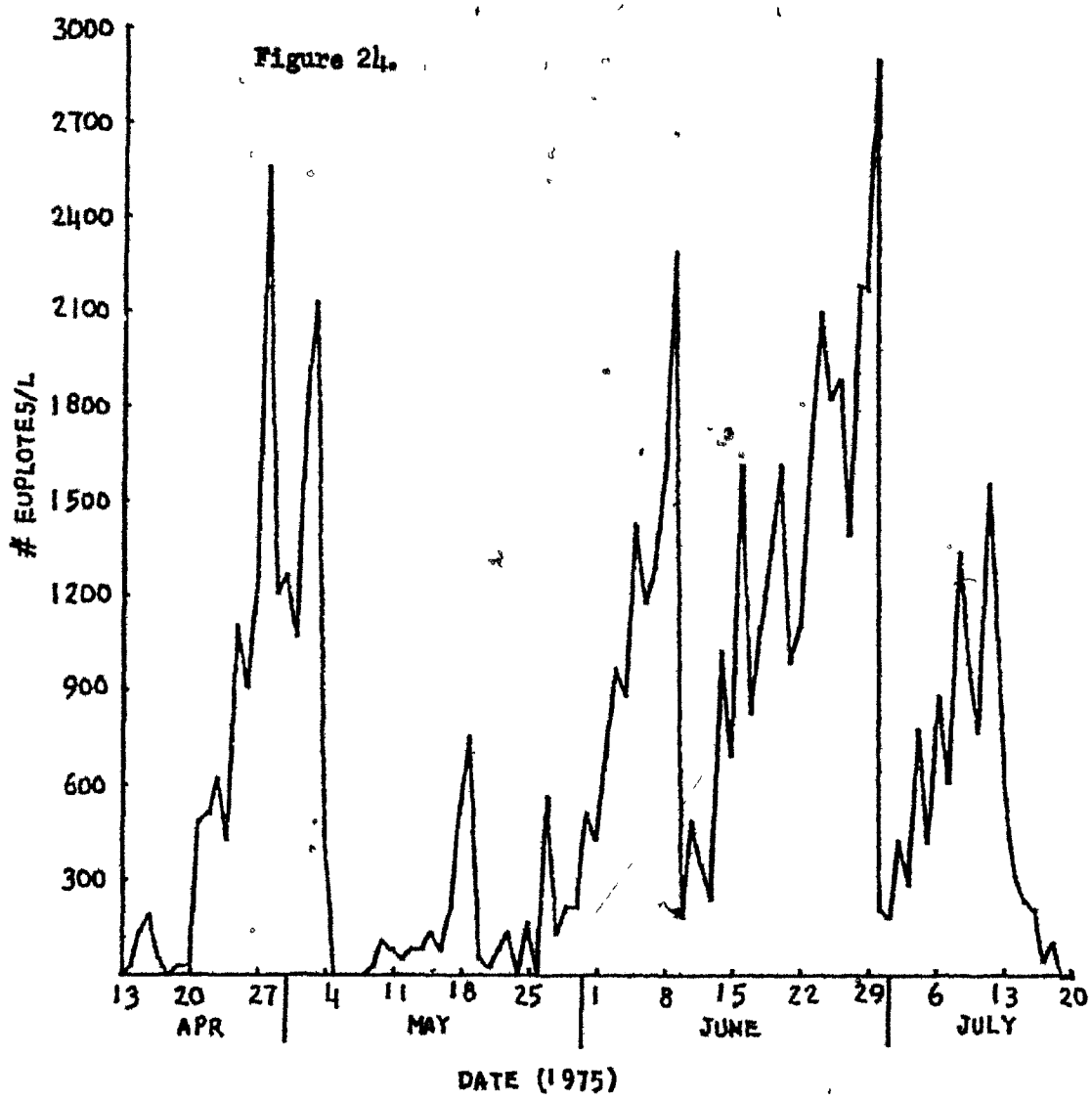


Figure 25.

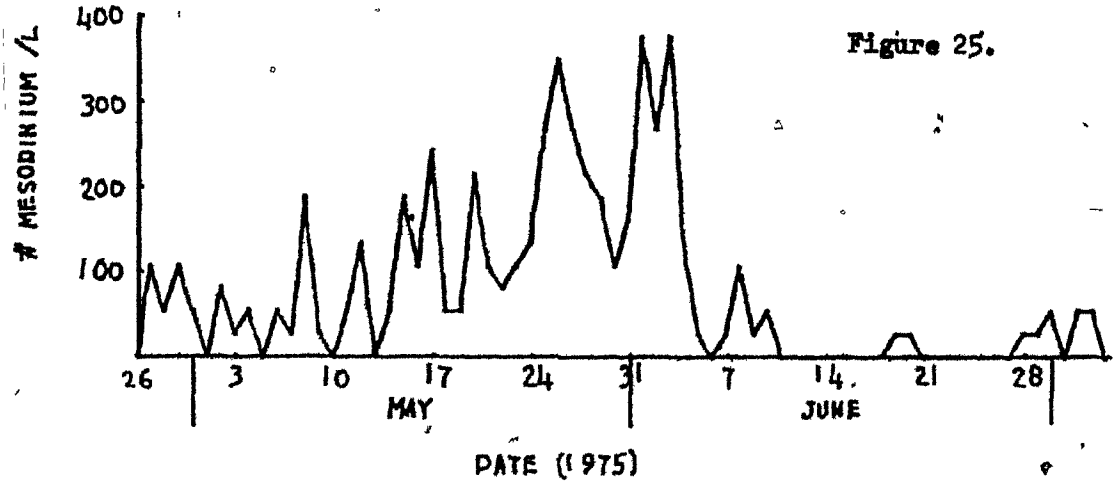


Figure 26.

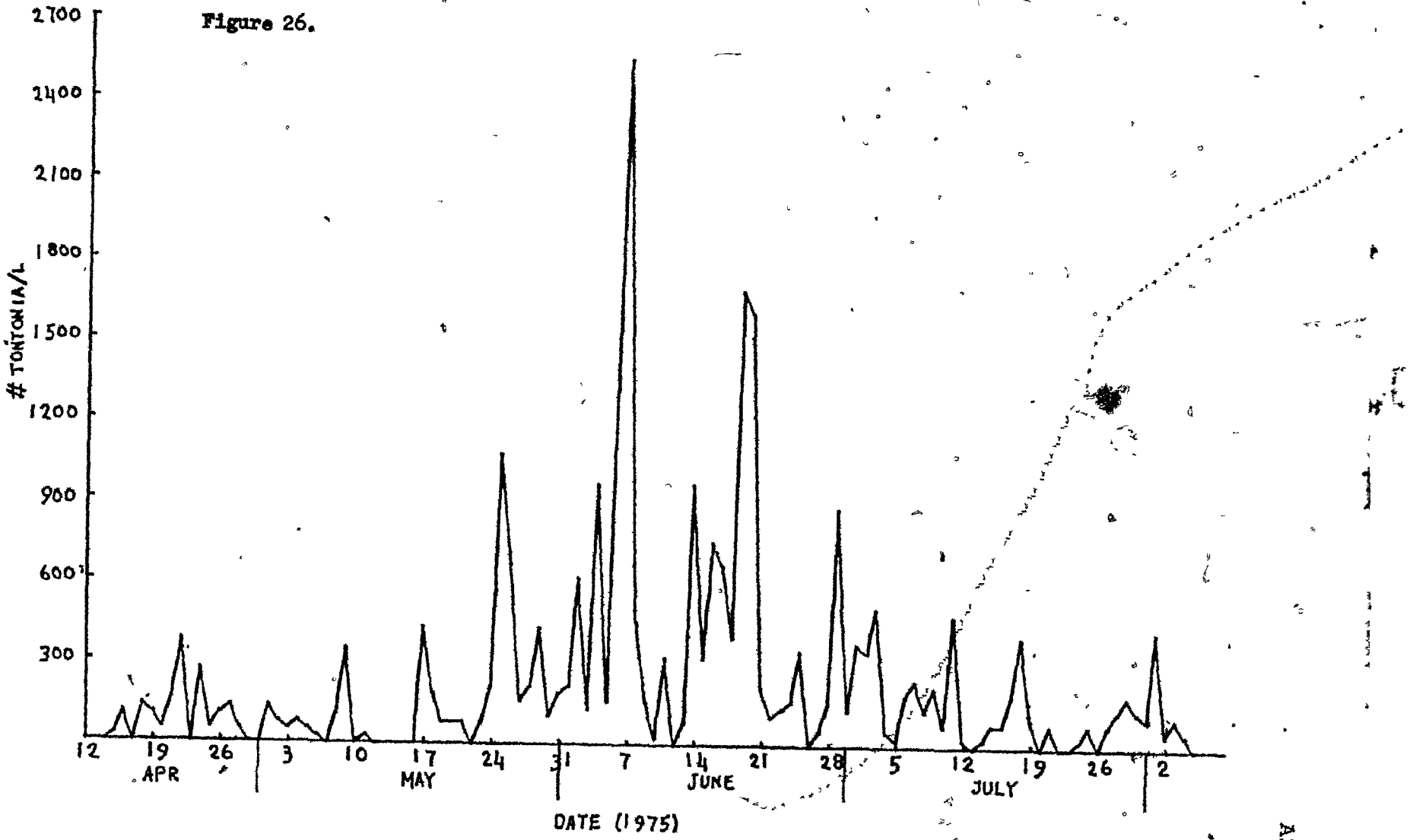

2700
2400
2100
1800
1500
1200
900
600
300
TONTONIA/L
12
19
26
APR
3
10
17
MAY
24
31
7
14
JUNE
21
28
5
12
19
JULY
26
2
DATE (1975)

Figure 27.

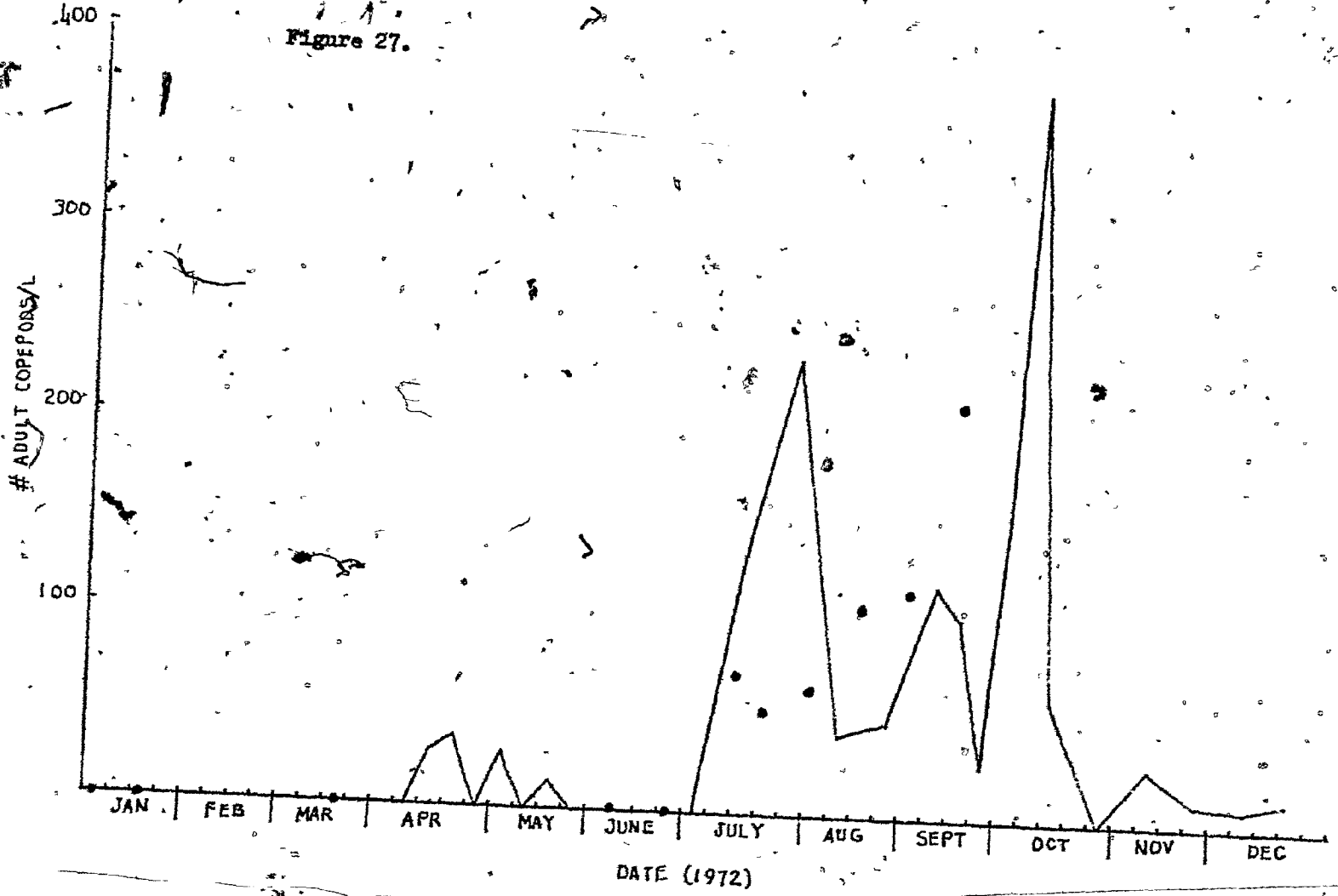

400
300
200
100
ADULT COPEPODS/L
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
DATE (1972)

Table 1. NWA protozoa abundance (#/l): 1972-1974. Strombidium sp. (S.sp.), Strombidium clakinsi (S.cal.), Strombidium conicum (S.con.), Strombidium strobilus (S.str.), Strombidium sulcatum (S.sul.), Tontonia gracillima (T.g.), Cyclotrichium meunieri (C.m.).

DATE	S.SP.	S.CAL.	S.CON.	S.STR.	S.SUL.	T.G.	C.M.
16 Mar 72	1226				626		
22 Mar 72	1889		28		57	71	386
29 Mar 72	5694	27	37	37	229	825	2322
5 Apr 72	3926				85		2558
12 Apr 72	825						4100
19 Apr 72	4692	36	100				748
26 Apr 72	2791	57	722	85	1104		864
3 May 72	2582	634	42	67	402	42	4441
10 May 72	6241	684	637	64	57	166	7830
17 May 72	3658	115	65	302	13	20	12256
24 May 72	2792	238	142	44	336	253	9543
31 May 72	1403		134		2148		3087
4 June 72	7617	121	2190	806	1384	40	5588
28 June 72	8436		242		3610	174	5698
12 July 72	9820			14	7538		3520
26 July 72	10491				7978	14	2303
9 Aug 72	247		54		2158	24	654
23 Aug 72	784	12	225		3694	25	190
6 Sept 72	1518	340	168		3326	140	332
13 Sept 72	173	14	14		643		1154
20 Sept 72	2507	483			2081	855	3738
27 Sept 72	186	120	59		3057	282	474
4 Oct 72	186	228	54		91	144	2880
11 Oct 72	687	44	128		2020	1167	15227
25 Oct 72	36431	970	662		14		4302
8 Nov 72	356	63	948		552	12	2538
22 Nov 72	300		13	11	450	24	891
6 Dec 72	308		128		155	10	42
18 Dec 72	821			4	497	4	536
4 Jan 73	1073		22		340	22	63
17 Jan 73	533		578	27	697		1226
5 June 73	15756	708	533	165	2185	255	8844
20 June 73	1578		179	14	2320	1248	7307
10 July 73	1244	6	256		1782	328	5912
18 July 73	14624	34	706		248	54	21321
1 Aug 73	3384		668		4637	124	8813
15 Aug 73	849	34	68		6124	60	725
29 Aug 73	2025	76	982	4	5796	120	550
12 Sept 73	556	18	333	9	1545	302	5436
19 Dec 73					376		268
10 Jan 74					5685		537
25 Jan 74					922		
1 Feb 74					483		

Table 1. (continued)

DATE	S.SP.	S.CAL.	S.CON.	S.STR.	S.SUL.	T.G.	C.M.
22 Feb 74					9887		54
1 Mar 74	89		18	24	10883		72
8 Mar 74	94		148		1557		134
15 Mar 74	14		27		1074	14	54
22 Mar 74	54	18	197		13497	36	895
29 Mar 74	27	134	268		10146		134
5 Apr 74	81	54	188		1611	108	27
17 Apr 74	107		268		430		
24 Apr 74	376	121	349		2635	202	27
5 May 74	107	322			107		322
15 May 74	27	54		54	134	27	
29 May 74	394	72	18		1378		1450
11 June 74	626	286	161	54	1915	161	3601
26 June 74	304	36	215	90	555	573	6945
11 July 74				36	3222		1181
25 July 74					20621		
1 Aug 74					644		107
7 Aug 74					2219		143
22 Aug 74					2255		107
24 Aug 74		54			19225		430
27 Aug 74					9210		80
4 Sept 74	268	322		322	8216		10633
5 Sept 74	161	27			3920	242	17372
12 Sept 74	107	161			1504		11116
18 Sept 74		54			967	54	14177
25 Sept 74	143	18	54		1826		12083
26 Sept 74	537		107		1611	537	9666
7 Oct 74	54		54		107		54
10 Oct 74					215		1665
11 Oct 74	268				3866	618	8270
29 Oct 74	107				81	27	537
31 Oct 74	1799	134			14096		3598
7 Nov 74	349				4430	54	4564
14 Nov 74	27				295		510
22 Nov 74	107				161		81
28 Nov 74	215				107		2041
5 Dec 74					242		806
12 Dec 74	161			27	134	81	376

Table 2. NWA tintinnid abundance (#/l): 1972-1974. Helicostomella subulata (H.S.), Leprotintinnus pellucidus (L.P.), Parafavella gigantea (P.G.), Tintinnopsis karajacensis (T.K.), Tintinnopsis parvula (T.P.), Tintinnopsis sacculus (T.SAC.), Tintinnopsis strigosa (T.STR.).

DATE	H.S.	L.P.	P.G.	T.K.	T.P.	T.SAC.	T.STR.
16 Mar 72					20		
22 Mar 72					14		
29 Mar 72					71		
5 Apr 72					52		
12 Apr 72				24	825		
19 Apr 72			36		71		
26 Apr 72					28		28
10 May 72					100		
17 May 72					54		
24 May 72			20		71		
4 June 72	40			14	94		295
28 June 72	202			27	524		843
12 July 72	4981		134		1181		81
26 July 72	17178		959	14	53706		14
9 Aug 72	4176		234		164		
23 Aug 72	1106				237		
6 Sept 72	2250				32		
13 Sept 72	413		7		417		
20 Sept 72	2176						
27 Sept 72	2864		28		12		
4 Oct 72	1015				7		
11 Oct 72	560				912		
25 Oct 72	246				1526		192
8 Nov 72	31				2930		
22 Nov 72	25				627		
6 Dec 72	18				507		
18 Dec 72	21				269		
[illegible] 73	9				49		
[illegible] 73	18				9		4
[illegible] 73		280			14		371
[illegible] June 73		81			69		81
16 July 73	777				24		24
18 July 73	235	14	14		257		
1 Aug 73	1243		110		237		32
15 Aug 73	1766		240				
29 Aug 73	1543		37	4	67		
12 Sept 73	374		9		128		
19 Dec 73					54		
25 Jan 74					54		
8 Mar 74						27	
15 Mar 74						14	
22 Mar 74	18						

Table 2. (continued)

DATE	H.S.	L.P.	P.G.	T.K.	T.P.	T.SAC.	T.STR.
29 Mar 74				28			27
5 Apr 74					54		
24 Apr 74		14		14	54		40
5 May 74		913		268		107	5800
15 May 74		2228		27	54		590
29 May 74		108					72
11 June 74		72		18		36	36
26 June 74	555	18		125	18	2238	161
11 July 74	967					430	
25 July 74	2309						
1 Aug 74	6324		52				
7 Aug 74	1897						18
22 Aug 74	2900						
24 Aug 74	4296						
27 Aug 74	2228						
4 Sept 74	430						
5 Sept 74	3652		27			54	
12 Sept 74	1074						
18 Sept 74	376						
25 Sept 74	1880						
26 Sept 74	1718				215	322	
7 Oct 74	376						
10 Oct 74	537						
11 Oct 74	295				81		
29 Oct 74	134				483		
31 Oct 74	54				215		
7 Nov 74	54				242		
14 Nov 74	134				510		
22 Nov 74	54				376		
28 Nov 74	54				81		
5 Dec 74					54		
12 Dec 74					134		

APPENDIX B

Figure 1. Strombidium sp. Diameter ≈30 µ. Lorica spherical, very delicate, extending over the major portion of the body.

Figure 2. Strombidium calkinsi (Faure-Fremiet). Length ≈100 µ. Diameter ≈80 µ. Lorica conical, very delicate and hyaline; caudal process present.

Figure 3. Strombidium conicum (Lohmann). Length 40-75 µ. Diameter 35-55 µ. Lorica conical with fine longitudinal lines; fundus acutely rounded.

Figure 4. Strombidium strobilus (Lohmann). Length 80-97 µ. Diameter 55-68 µ. Lorica helical with 4 or 5 coils; peristome more or less contractile.

Figure 5. Strombidium sulcatum. Length 20-30 µ. Diameter 10-20 µ. Lorica delicate, conical, covering only the posterior portion of the body.

Figure 6. Helicostomella subulata (Ehrenberg). Length 150-340 µ. Diameter 20-27 µ. Long narrow cylinder contracting gradually to slender, often slightly curved pedicel; 1-41 spiral turns in upper part; upper edge of spiral band denticulate.

Figure 7. Leprotintinnus pellucidus (Cleve). Length 147-300 µ. Diameter 40-50 µ. Lorica more or less cylindrical, open aboral end narrower than oral often after a slightly constricted area; sparsely agglomerated.

Figure 8. Parafavella gigantea (Brandt). Length 270-520 µ. Diameter 61-68 µ. Elongate, cylindrical, sometimes with slight flaring mouth; pedicel up to ¼ total length; oral rim denticulate; hexagonal reticulation absent on pedicel.

Figure 9. Tintinnopsis karajacensis (Brandt). Length 67-127 µ. Diameter 47-50 µ. Cylindrical with rounded aboral end; sometimes slightly expanded at mouth and lower part of bowl; arenaceous.

Figure 10. Tintinnopsis parvula (Jorgensen). Conjugating pair at right. Length 40-90 µ. Diameter 37-43 µ. Slightly expended below anterior region; pointed aborally; arenaceous.

Figure 11. Tintinnopsis sacculus (Brandt). Length 67-203 µ. Diameter 40-67 µ. Cylindrical, with rounded aboral end; sparsely agglomerated.

Figure 12. Tintinnopsis strigosa (Meunier). Length 43-153 µ. Diameter 33-40 µ. Cylindrical with sharply pointed conical aboral end.

Figure 13. Cyclotrichium meunieri (Bary and Stuckey). Sketch of the animal in the living state. Length 80-100 µ. Diameter 19-41 µ. Anterior half domelike, posterior half extended; greenish-maroon chromatophores; broad ciliated band around middle.

Figure 14. Cyclotrichium meunieri. Animal preserved with Champy's fixative.

Figure 15. Euplotes sexcostatus. Length 50-80 µ. Diameter 33-58 µ. Body broadly ovoid, compressed; dorsal side with 6 longitudinal ribs, ventral side with 9 anterior and 6 posterior cirri.

Figure 16. Mesodinium pulex (Claparede and Lackmann). Length 21-38 µ. Movement rapid and sudden; when stationary has the appearance of a heliozoan; colourless; central rows of cilia; tentacle-like retractile process around cytostome.

Figure 17. Tontonia gracillima (Faure-Fremiet). Length 48-52 µ. Caudal process about equal to the body length.

Figure 18. Tintinnopsis karajacensis with at least 11 Rhodomonas lens inside. Animal length ≈100 µ; diameter ≈50 µ.

Figure 19. Parafavella gigantea with almost the entire body occupied by Dunaliella cells. Lorica length ≈390 µ; diameter ≈65 µ. Animal length ≈150 µ; diameter ≈60 µ.

Figure 20. Tintinnopsis tubulosoides, freshly collected, 14 Jan 1975. Lorica length 84 µ.

Figure 21. Tintinnopsis tubulosoides, 18 Jan 1975. Lorica length 80 µ.

Figure 22. Tintinnopsis tubulosoides, 29 Jan 1975. Lorica length 50 µ.

Figure 23. Tintinnopsis tubulosoides, 5 Feb 1975. Lorica length 32 µ.

Figure 24. Tintinnopsis tubulosoides, 18 Feb 1975. Lorica length 17 µ.

Figure 25. Helicostomella subulata cyst.

Figure 26. Leprotintinnus pellùcidus cyst.

Figure 27. Acanthostomella norvegica cyst.

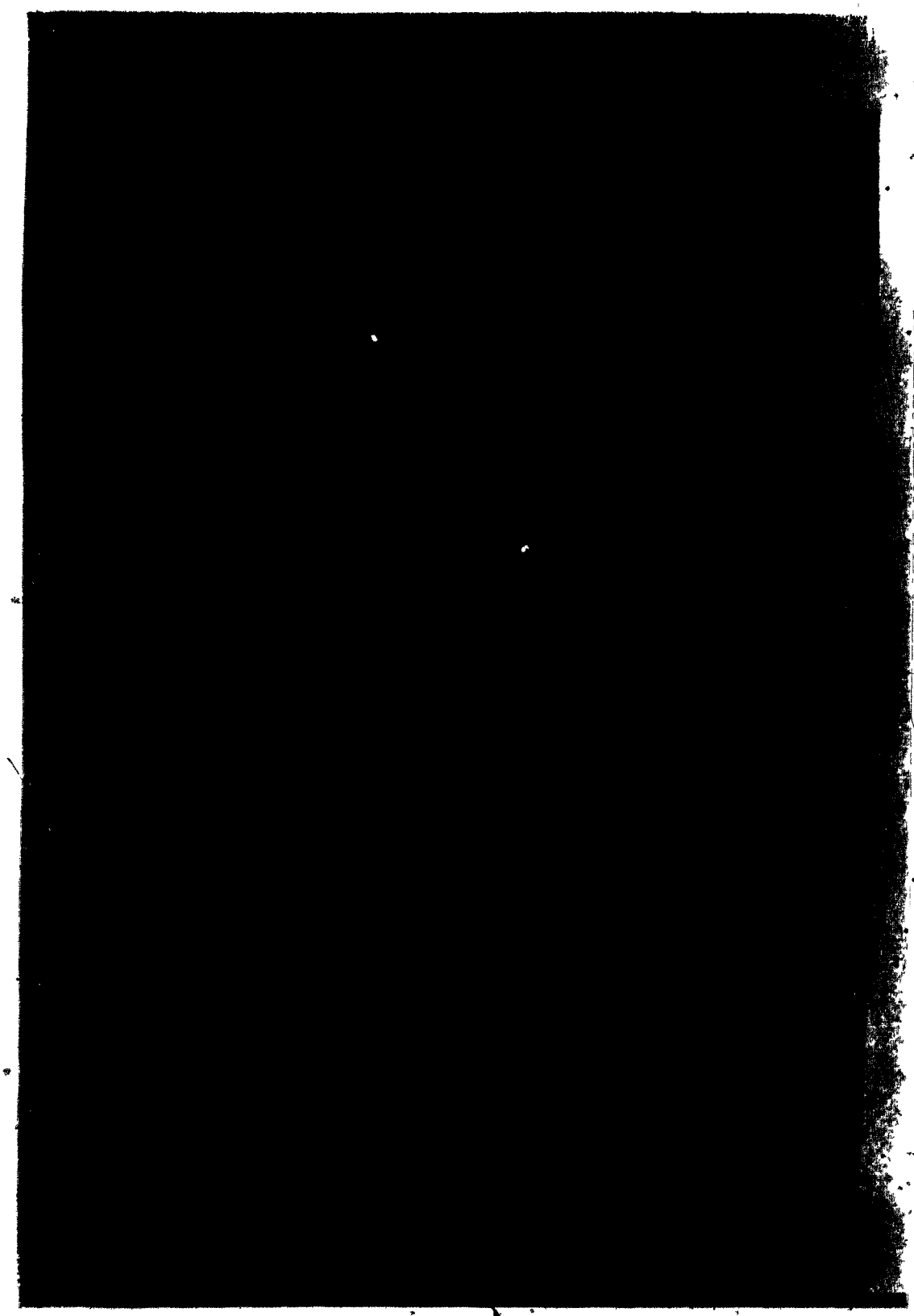
Figure 28. Helicostomella subulata "spores".

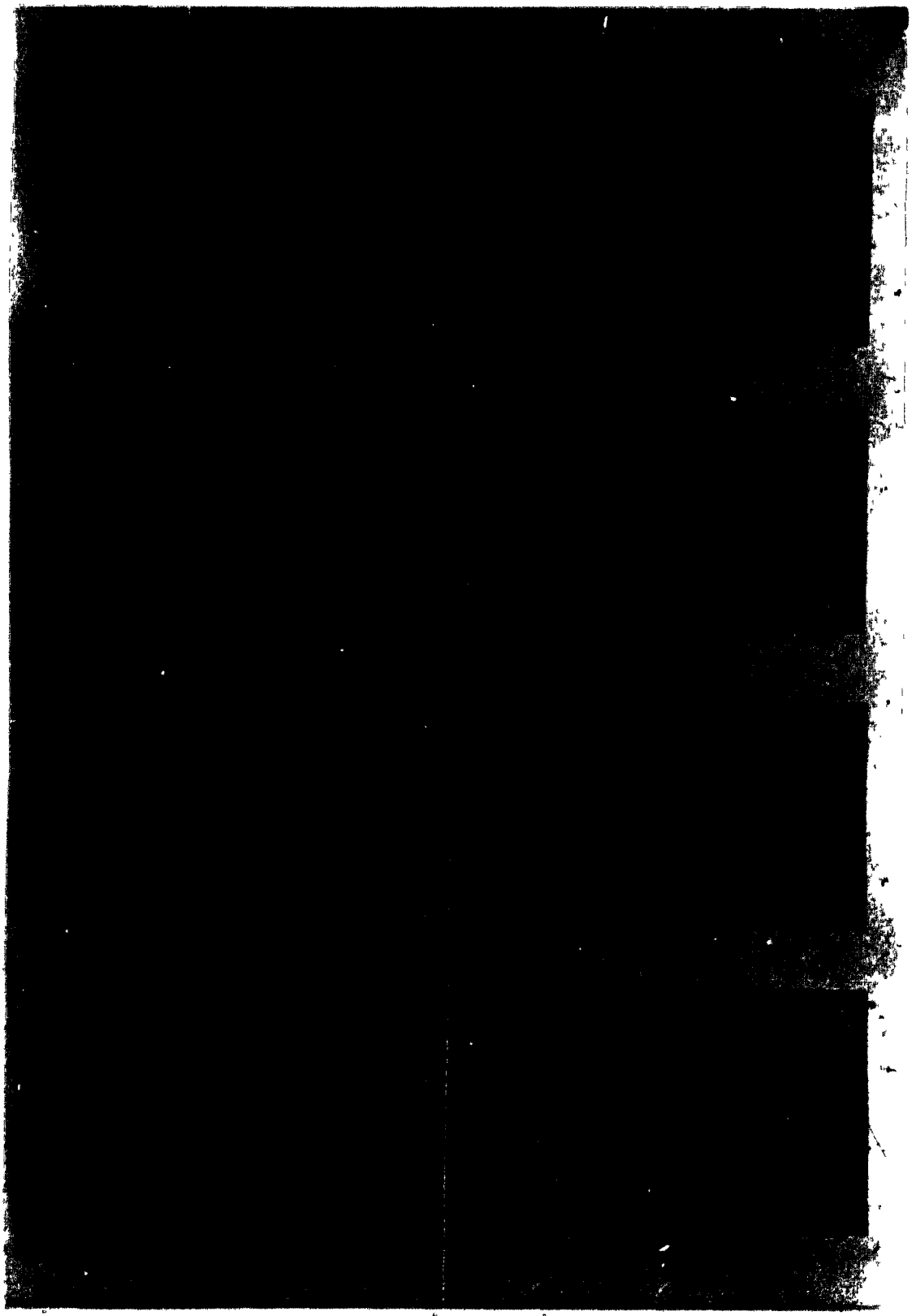
Figure 29. Helicostomella subulata "spores".

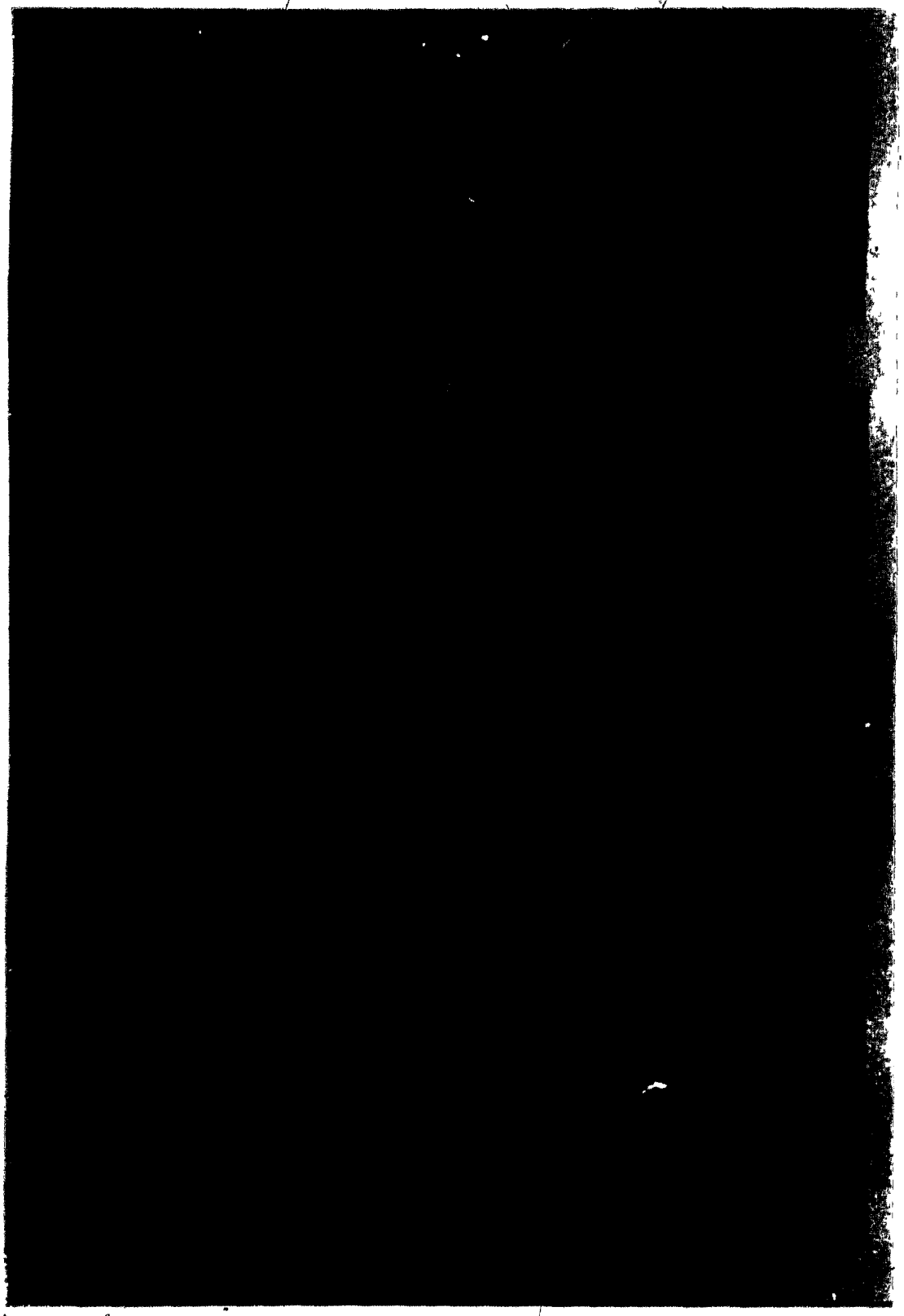
Figure 30. Tintinnopsis parvula showing addition of material at the oral opening prior to division. Lorica length 77 µ.

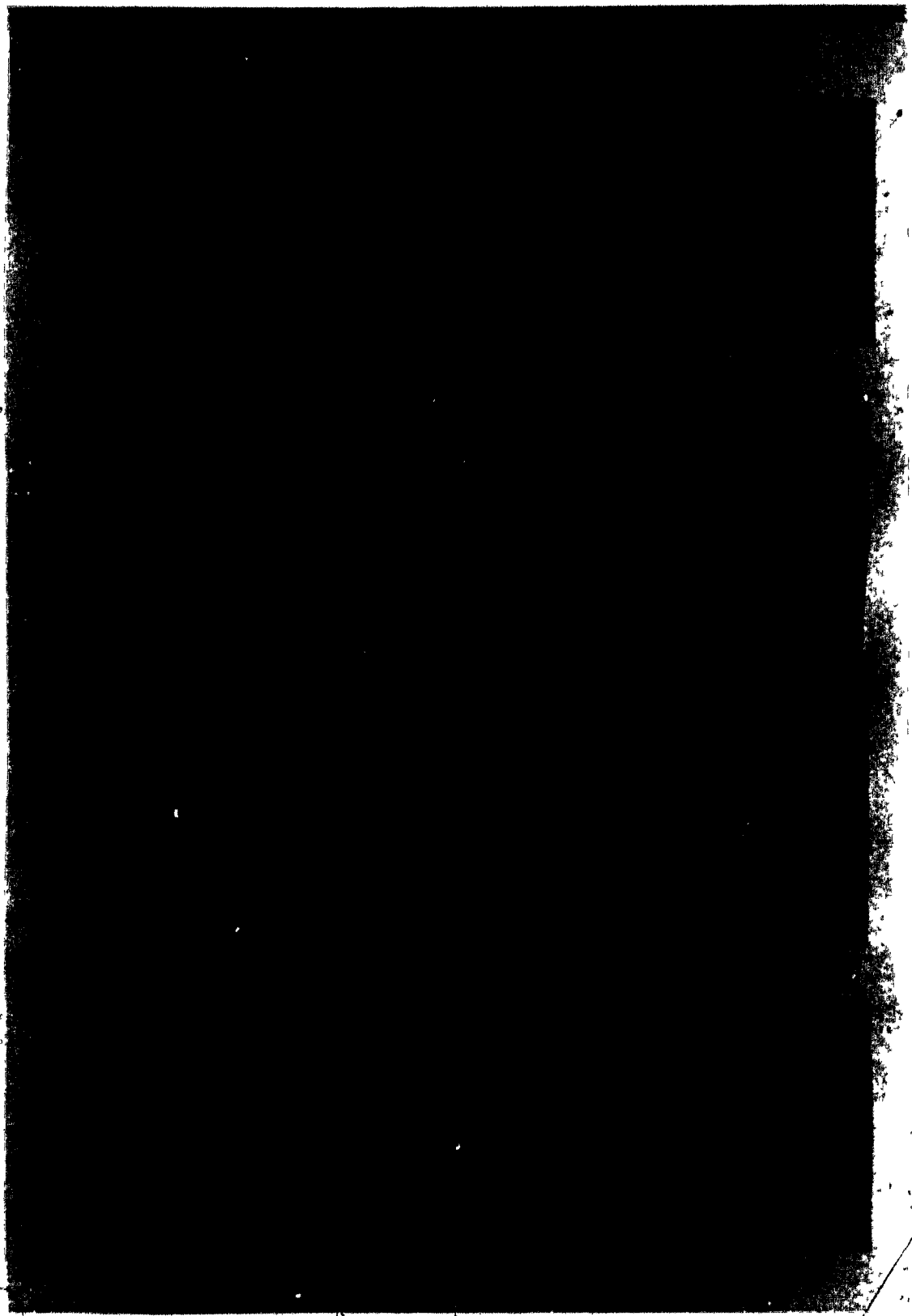
Figure 31. Tintinnopsis strigosa showing addition of material to the oral opening prior to division. Lorica length 80 µ.

Figure 32. Two individuals of Tintinnopsis sacculus in one lorica. Lorica length 220 µ.









APPENDIX C

TABLE 1. SPECIES MAXIMUM ABUNDANCE (#/L), STATION (ST) AND DEPTH (Z) LOCATION

SPECIES	MARCH (SSIII) #/L	ST	Z(m)	JUNE (SSI) #/L	ST	Z(m)	AUGUST (SSIV) #/L	ST	Z(m)	NOVEMBER (SSII) #/L	ST	Z(m)
Difflugia oblonga							27	5	50	18	2	0
										18	3	0
Euglypha laevis	13	7	6				40	7	8	36	1	10
Candeina nitida				18	5	80						
				18	5	0						
Globigerina bulloides	13	7	100				13	3	200	18	3	200
										18	4	10
Astrosphaera hexagonalis							13	3	50	18	3	25
Coelacantha dogiella										18	3	75
Coelodenorum furcatissimum										18	4	0
Lithomelissa setosa	54	7	200	54	7	50	27	7	50	27	4	50
Phormacantha hystrix										18	3	75
Stichocorythe zanclea	13	1	50	36	7	100	134	7	30	18	6	25
	13	1	75									
	13	7	0									
	13	7	0									
Triplagia primordialis							54	3	50	18	3	200
Xiphosphaera vesta							27	3	25			
Cyclotrichium meunieri	201	7	0	501	2	25	362	7	30	3258	7	1
Didinium nasutum	27	2	0				671	7	30	36	4	50
										36	5	0
										36	5	25
Lacrymaria alor										36	4	0
Mesodinium pulex							81	1	0	90	3	25
Mesodinium rubrum							27	1	10	107	3	25
Tiarina fusus	54	3	49				698	7	0	36	4	0
Frontonia marina	54	3	23				846	7	30	233	3	25
Strombidium sp.	242	7	0	2452	3	42	7343	1	0	734	6	0
Strombidium acuminatum	27	3	23	18	4	50	13	3	250	18	5	0
										18	6	10
Strombidium calkinsi	67	3	0	72	5	21	13	7	75	72	5	10
							13	7	250	72	5	25
Strombidium cornucopiae										36	4	10

Table 1. (continued)

SPECIES	MARCH (SSIII) #/L	ST	Z(m)	JUNE (SSI) #/L	ST	Z(m)	AUGUST (SSIV) #/L	ST	Z(m)	NOVEMBER (SSII) #/L	ST	Z(m)
Strombidium conicum	349	3	0	1396	2	0	980	7	30	2178	4	0
Strombidium ovale	67	4	25	36	4	50	5974	5	30	107	6	10
				36	4	70						
Strombidium strobilus	134	5	13	251	5	0	201	7	10	72	6	0
	134	5	20									
Strombidium sulcatum	1114	6	0	1002	2	0	5169	7	50	1396	3	0
Strombidium typicum							416	5	10	72	5	10
Tontonia gracillima	134	3	49	1504	6	0	658	5	23	251	6	10
Acanthostomella norvegica	94	5	20	304	7	50	309	13	50	286	4	10
Acanthostomella conicoides							470	13	0	18	7	1
Amphorella gaaderae							18	7	0			
Amphorella quadrilineata	27	7	100	36	7	2.5	1665	1	0	609	3	0
Ascampbella urceolata				36	7	100						
Climacocylis scalaroides							13	5	10			
Codonella acuta										125	2	10
Codonellopsis contracta	40	6	150	54	6	150						
				54	7	50						
Dadayiella bulbosa							255	3	0			
Dictyocysta elegans										18	5	0
Dictyocysta reticulata							40	7	50			
Dictyocysta speciosa				54	7	50						
Epiplocylis acuminata							36	7	0			
Eutintinnus fraknoi							134	7	17			
Favella franciscana				18	6	50						
				18	6	75						
				18	6	100						
Helicostomella subulata				18	2	50				27	1	25
				18	5	42						
				18	6	150						
Metacylis corbula				125	6	50				90	1	10

Table 1. (continued)

SPECIES	MARCH(SSIII) #/L	ST	Z(m)	JUNE(SSI) #/L	ST	Z(m)	AUGUST(SSIV) #/L	ST	Z(m)	NOVEMBER(SSII) #/L	ST	Z(m)
Parafavella edentata	13	1	10				13	1	50			
	13	6	0				13	5	4.5			
	13	6	75				13	5	50			
	13	7	0				13	5	75			
Parafavella gigantea	13	2	10				13	1	50	18	3	50
	13	2	25				13	2	75			
Parafavella parumdentata	27	1	50	72	7	2.5				36	4	25
	27	5	0									
	27	6	50									
Parundella grandis							27	7	30			
Parundella major	13	7	150	90	7	100	27	7	75			
	13	7	200									
Parundella minor				18	2	75						
				18	7	200						
Parundella subcaudata							27	7	15			
Poroecus curtus	13	7	47									
Proplectella globosa							2323	1	0			
Proplectella parva				36	7	100						
Proplectella perpusilla										36	4	0
Proplectella subacuta	13	5	75	18	5	80						
Proplectella subcaudata							13	7	100			
Proplectella tumida	13	1	0							18	3	100
Protorhabdonella curta	13	7	0	125	7	2.5	362	5	0	36	4	10
										36	6	0
Ptychocylis drygalskii	27	1	75	18	3	200				36	3	25
				18	6	0						
Ptychocylis minor	13	7	6									
Salpingella accuminata				430	7	50						
Salpingella curta				18	7	50						
Salpingella gracilis							27	7	50			
Stenosemmela ventricosa							242	2	25			

Table 1. (continued)

SPECIES	MARCH(SSIII) #/L	ST	Z(m)	JUNE(SSI) #/L	ST	Z(m)	AUGUST(SSIV) #/L	ST	Z(m)	NOVEMBER(SSII) #/L	ST	Z(m)
Stenostrupiella steenstrupii							510	5	10			
Tintinnopsis cylindrica							13	7	8			
Tintinnopsis lata				36	5	80				72	2	10
				36	6	150						
Tintinnopsis parvula	40	1	10									
Tintinnopsis pistilum										18	4	0
Tintinnopsis sacculus				18	6	0	13	1	50			
Tintinnopsis strigosa										18	3	25
Tintinnopsis undella				54	6	23				54	3	25
Tintinnus tubulosus				18	6	0	188	13	0	18	3	0
				18	7	50				18	7	1
Undella columbiana							188	3	15	268	3	0
Undellopsis pacifica				72	7	150						
Euplotes sexcostatus	980	1	25									
Tricophrya columbiae							13	5	15			

TABLE 2. SUMMARY OF TOTAL NUMBER OF PROTOZOA PER LITER

CRUISE	Z(m)	STATION NUMBER 1	2	3	4	5	6	7
MARCH	0	295	886	1154	1503	430	1463	884
(SSIII)	10	489	1194	792	1074	549	1503	186
	25	1274	873	793	938	1060	766	444
	50	502	281	603	482	215	1046	375
	75	361	147		107	146	213	106
	100		200	65			227	119
	150						146	92
	200			67			26	160
JUNE	0	1415	2094	768	645	1271	2435	2078
(SSI)	10	699						
	25		1352	1226	618	770	859	
	50		1298	2524	2453	609	1145	2525
	75		422	1030	430	510	54	
	100		304	556			144	987
	150			180			162	288
	200			198			162	485
AUGUST	0	15370	6592	5570		8430		4035
(SSIV)	10	9586	6591	5704		10362		2737
	25	2939	6630	1987		12124		1354
	50	1675	1502	577		1867		10559
	75	591	750			588		347
	100		336	577				186
	150			147				159
	200			307				133
	250			133				137
NOVEMBER	0	1559	1541	2042	3428	1146	2385	5335
(SSII)	10	2365	1478	985	1881	1736	2132	1559
	25	878	449	1129	788	2650	1003	
	50	104	305	466	274	681	448	
	75			180	358			
	100			117				
	150			81				
	200			45				

TABLE 3. SUMMARY OF THE NUMBER OF SPECIES FOUND

CRUISE	Z(m)	STATION NUMBER 1	2	3	4	5	6	7
MARCH	0	8	10	10	9	6	9	10
(SSIII)	10	8	10	9	7	6	7	7
	25	9	10	9	8	7	7	6
	50	7	5	9	7	6	9	8
	75	7	5	10	3	6	8	5
	100		5	5			6	6
	150						7	5
	200			3			2	6
JUNE	0	6	7	5	6	8	10	14
(SSI)	10	4						
	25		5	7	5	5	9	
	50		7	7	8	6	9	13
	75		4	6	4	7	3	
	100		4	9			6	12
	150			5			5	9
	200			4			4	14
AUGUST	0	13	13	12		19		17
(SSIV)	10	10	12	12		19		14
	25	10	12	9		18		14
	50	13	10	8		10		20
	75	8	10			9		11
	100		6	7				8
	150			5				7
	200			10				6
	250			5				7
NOVEMBER	0	10	11	10	10	8	10	7
(SSII)	10	11	13	7	11	10	11	7
	25	8	7	9	9	10	11	
	50	5	5	7	6	7	7	
	75			6	2			
	100			4				
	150			4				
	200			2				

TABLE 4. SUMMARY OF SPECIES DIVERSITY INDICES

CRUISE	Z(m)	STATION NUMBER 1	2	3	4	5	6	7
MARCH	0	1.799	1.620	1.764	1.164	1.252	1.040	1.860
(SSIII)	10	1.497	1.353	1.728	1.419	1.380	1.228	1.722
	25	0.921	1.686	2.012	1.255	1.511	1.458	1.674
	50	0.800	1.175	1.868	1.493	1.633	1.370	1.769
	75	1.386	1.468		0.974	1.421	1.748	1.368
	100		1.263	1.609			1.498	1.672
	150						1.846	1.475
	200			1.055			0.693	1.633
JUNE	0	1.436	1.636	1.195	1.764	1.694	1.266	1.736
(SSI)	10	1.014						
	25		1.316	1.180	1.340	1.260	2.070	
	50		1.451	0.596	0.894	1.423	1.973	2.108
	75		1.179	1.056	0.866	1.415	1.098	
	100		0.901	1.851			1.668	2.205
	150			1.418			1.523	1.923
	200			1.162			1.273	2.418
AUGUST	0	1.377	1.261	1.377		1.700		1.901
(SSIV)	10	1.398	1.394	1.129		1.823		1.978
	25	1.189	1.396	1.165		1.752		2.056
	50	1.757	1.574	1.849		1.847		1.761
	75	1.721	1.699			1.699		2.119
	100		1.268	1.588				1.909
	150			1.444				1.589
	200			2.080				1.696
	250			1.418				1.621
NOVEMBER	0	1.778	2.012	1.792	1.591	1.635	1.710	1.056
(SSII)	10	1.832	1.971	1.532	1.742	1.899	1.753	1.129
	25	1.710	1.302	1.758	1.813	1.709	1.810	
	50	2.275	1.488	1.632	1.476	1.455	1.563	
	75			1.451	0.647			
	100			1.273				
	150			1.099				
	200			0.520				

TABLE 5. AVERAGE VALUES FOR THE TOP 50 METERS

	STATION NUMBER						
	1	2	3	4	5	6	7
A. Total number of protozoa							
March	640	809	836	999	564	1195	472
June	1057	1581	1506	1239	883	1480	2302
August	7393	5329	3460		8196		4671
November	1227	943	1156	1593	1553	1492	3447
B. Number of species							
March	8	9	9	8	6	8	8
June	5	6	6	6	6	9	14
August	12	12	10		17		16
November	9	9	8	9	9	10	7
C. Species diversity index							
March	1.254	1.459	1.843	1.333	1.444	1.274	1.756
June	1.225	1.368	0.990	1.333	1.459	1.770	1.922
August	1.430	1.406	1.370		1.781		1.924
November	1.899	1.693	1.679	1.656	1.672	1.709	1.093
D. Percentage of total protozoa comprised of tintinnids							
March	12	5	8	2	5	6	6
June	2	1	1	1	3	40	35
August	20	12	12		7		9
November	36	23	26	6	3	4	3
E. Percentage of total protozoa comprised of strombidia							
March	15	79	71	84	79	87	66
June	63	79	81	71	69	25	22
August	75	84	82		82		67
November	61	68	58	62	72	78	62

TABLE 6. AVERAGE VALUES FOR THE 50 - 250 METER LAYER

	STATION NUMBER						
	1	2	3	4	5	6	7
A. Total number of protozoa							
March	361	174	66	107	146	228	119
June		363	491	430	510	131	587
August	591	543	291		588		192
November		106	358				
B. Number of species							
March	7	5	8	3	6	6	6
June		5	6	4	7	6	12
August	8	8	7		9		8
November			4	2			
C. Species diversity index							
March	1.386	1.366	1.322	0.974	1.421	1.446	1.542
June		1.040	1.372	0.866	1.415	1.391	2.182
August	1.721	1.484	1.633		1.699		1.787
November		1.086	0.647				
D. Percentage of total protozoa comprised of tintinnids							
March	15	0	24	12	18	15	14
June		4	10	0	11	59	47
August	18	14	11		9		9
November			43	0			
E. Percentage of total protozoa comprised of strombidia							
March	26	81	40	50	73	54	50
June		88	80	96	78	28	39
August	64	68	49		82		66
November			36	100			

APPENDIX D

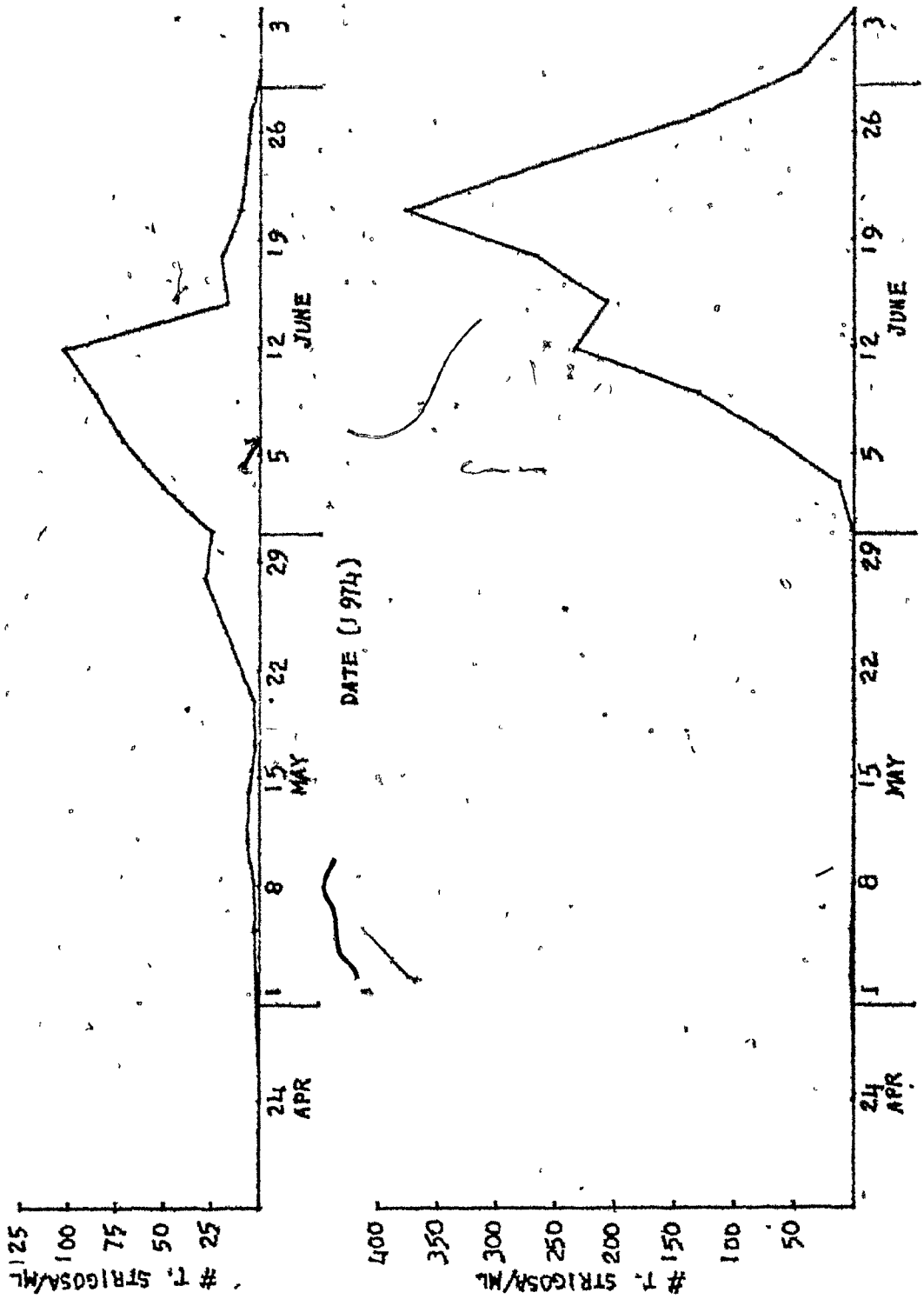

24 APR
1
8
15 MAY
22
29
5
12 JUNE
19
26
3
DATE (1974)
T. STRIGOSA/ML
125
100
75
50
25
400
350
300
250
200
150
100
50

Figure 1.

Figure 2.

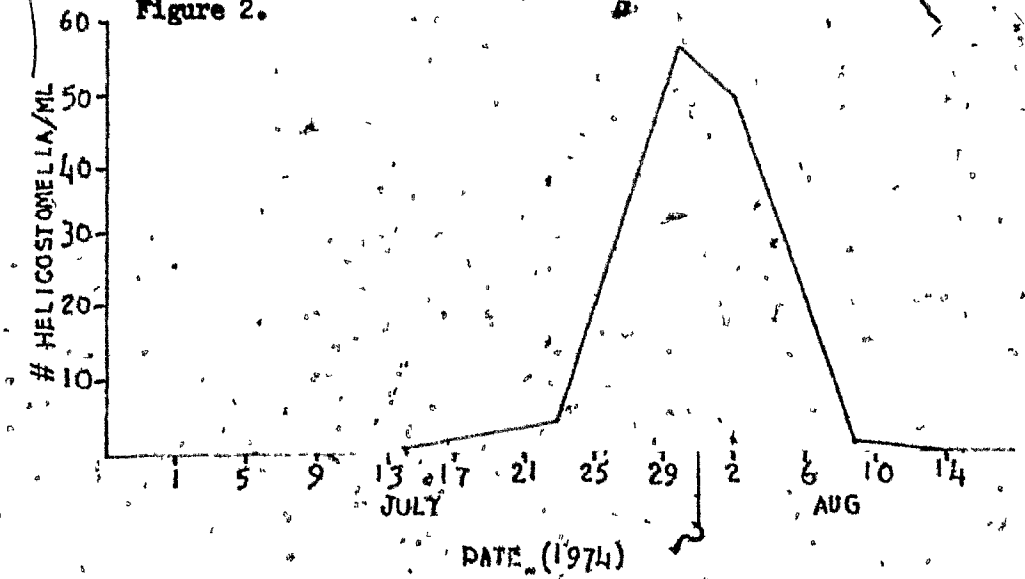


Figure 3.

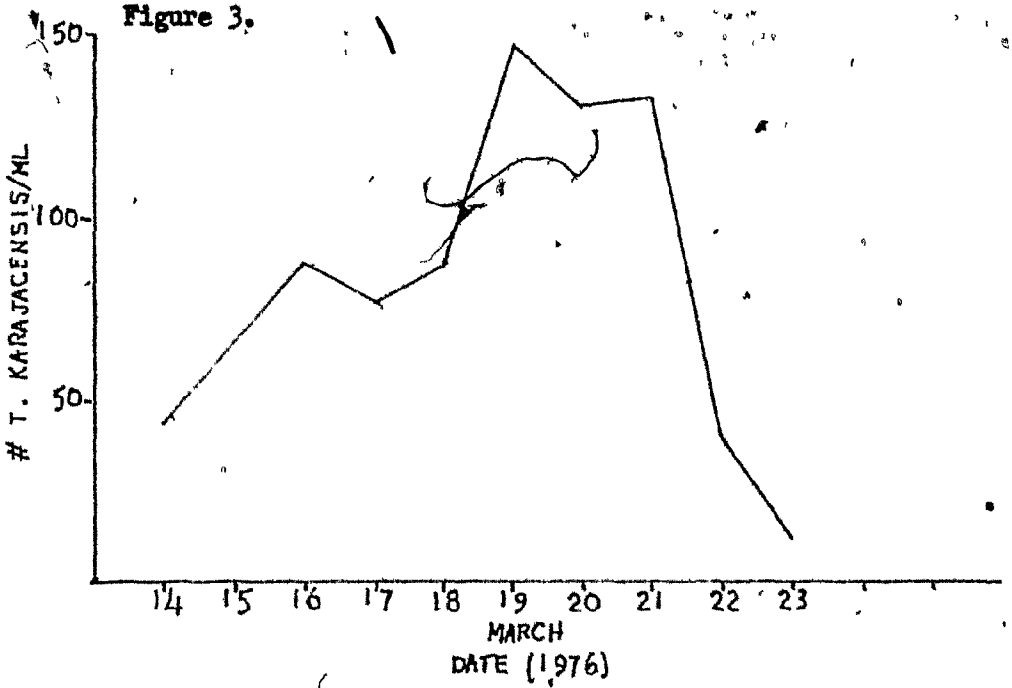


Figure 4.

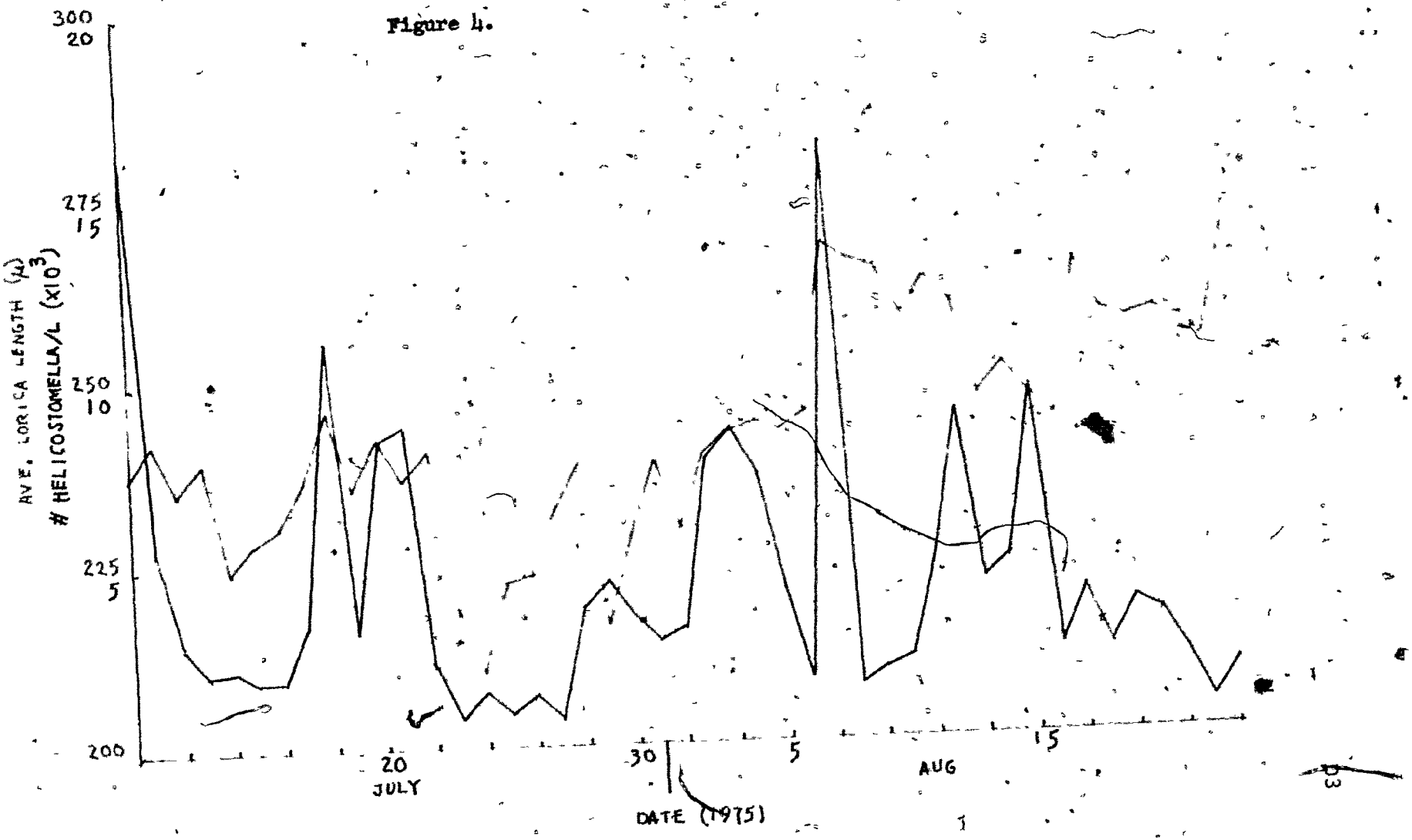

300
20
275
15
250
10
225
5
200
AVE. LORICA LENGTH (μ)
HELICOSTOMELLA/L (X10³)
20
JULY
30
5
AUG
15
DATE (1975)

Figure 5.

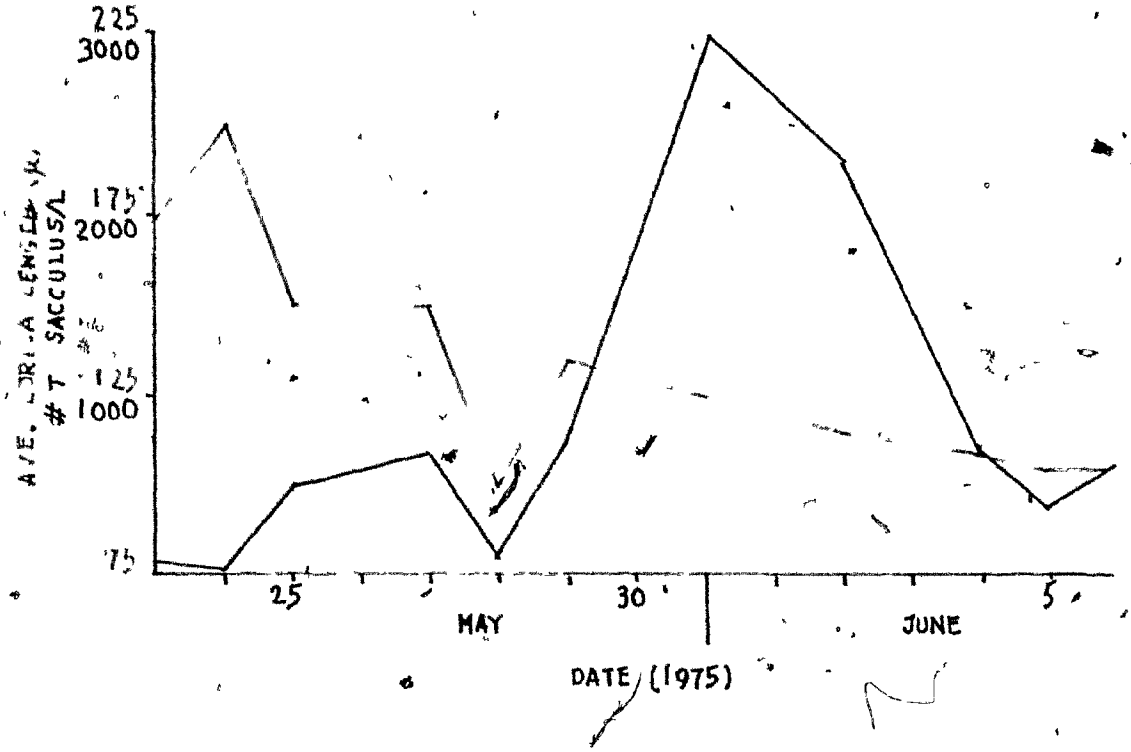


Figure 6a.

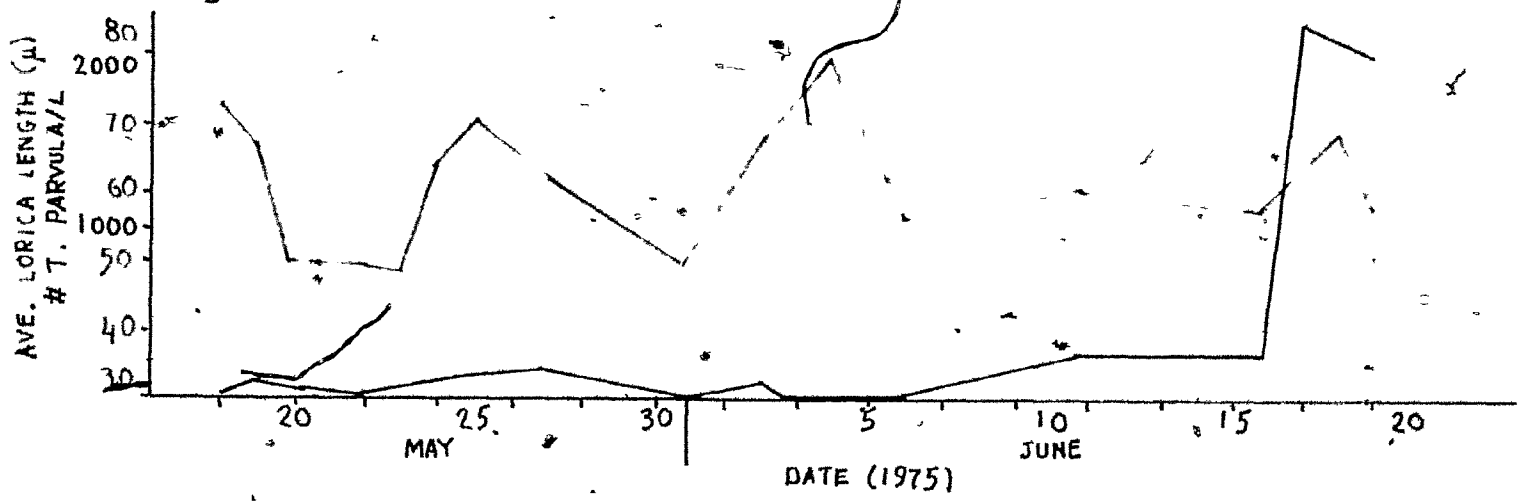


Figure 6b.

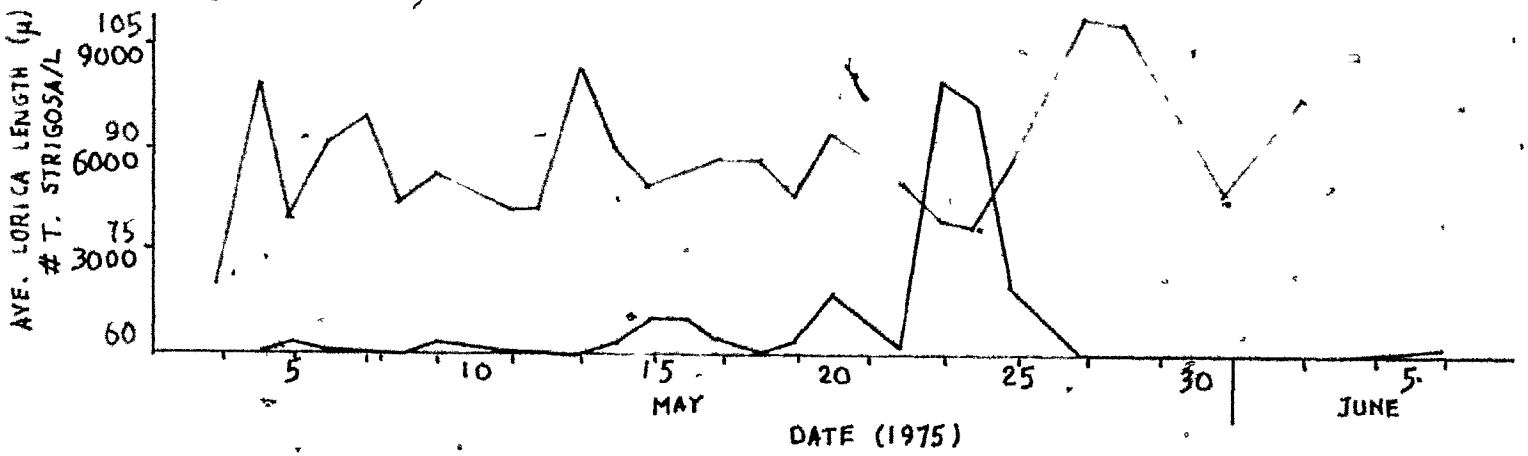


Figure 7a.

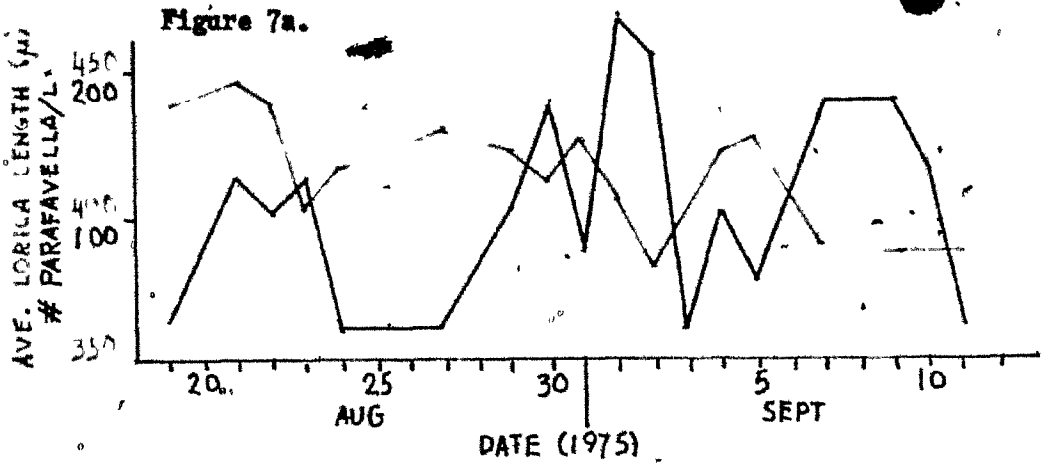


Figure 7b.

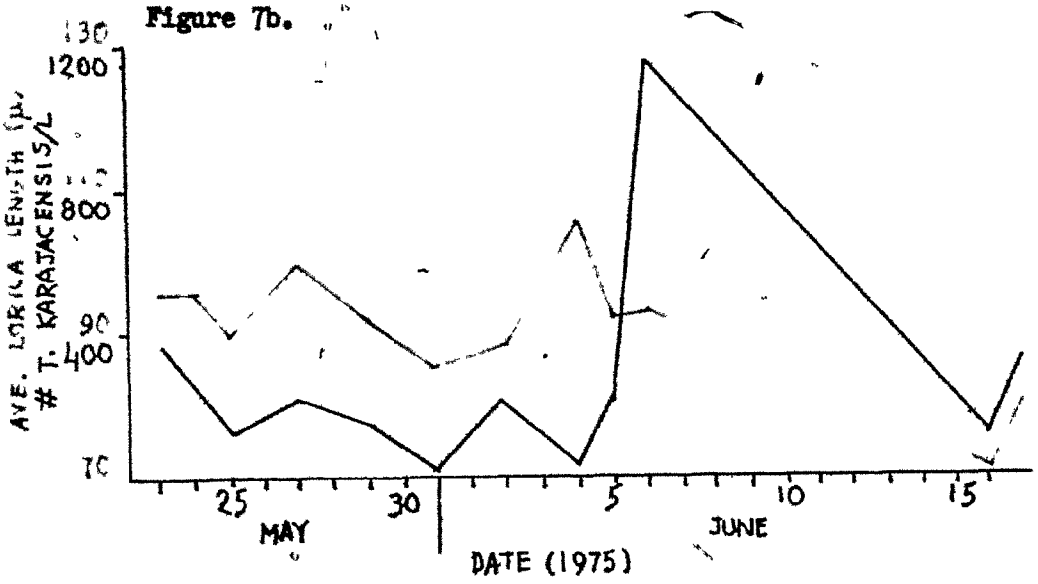


Figure 7c.